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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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DEPARTMENT OF [illegible]

EDMONTON, ALBERTA

[illegible]

UNIVERSITY OF ALBERTA

A STUDY OF TWO SPECIES OF GULLS, *LARUS CALIFORNICUS* AND *L. DELAWARENSIS*, BREEDING IN AN INLAND HABITAT.

by

KEES VERMEER

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
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UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "A Study of Two Species of Gulls, Larus californicus and L. delawarensis, Breeding in an Inland Habitat" submitted by Kees Vermeer in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

ABSTRACT

The breeding chronology, reproductive success, nesting habitat, food, helminth fauna, and growth rates of California Gulls (Larus californicus) and Ring-billed Gulls (Larus delawarensis) were studied at Miquelon Lake, Alberta in 1964 and 1965 in order to learn whether these species exhibit special adaptations to breeding in an inland environment.

Few basic differences were found between gull species breeding inland and those breeding on the seacoast. Both species at Miquelon Lake are ground nesters like many coastal species. Growth and reproductive rates of the California Gull and Ring-billed Gulls are similar to those of Glaucous-winged Gulls (Larus glaucescens) breeding on the coast of British Columbia.

Apparent adaptations of the two species to breeding inland are the ability to exploit a seasonally abundant supply of insects and rodents and a shortened breeding season. The short breeding season is marked by a compressed pre-egg period, a short laying period and a reduction of repeat laying. These adaptations appear to achieve maximum reproduction by making the most use of the seasonal nature of the food.

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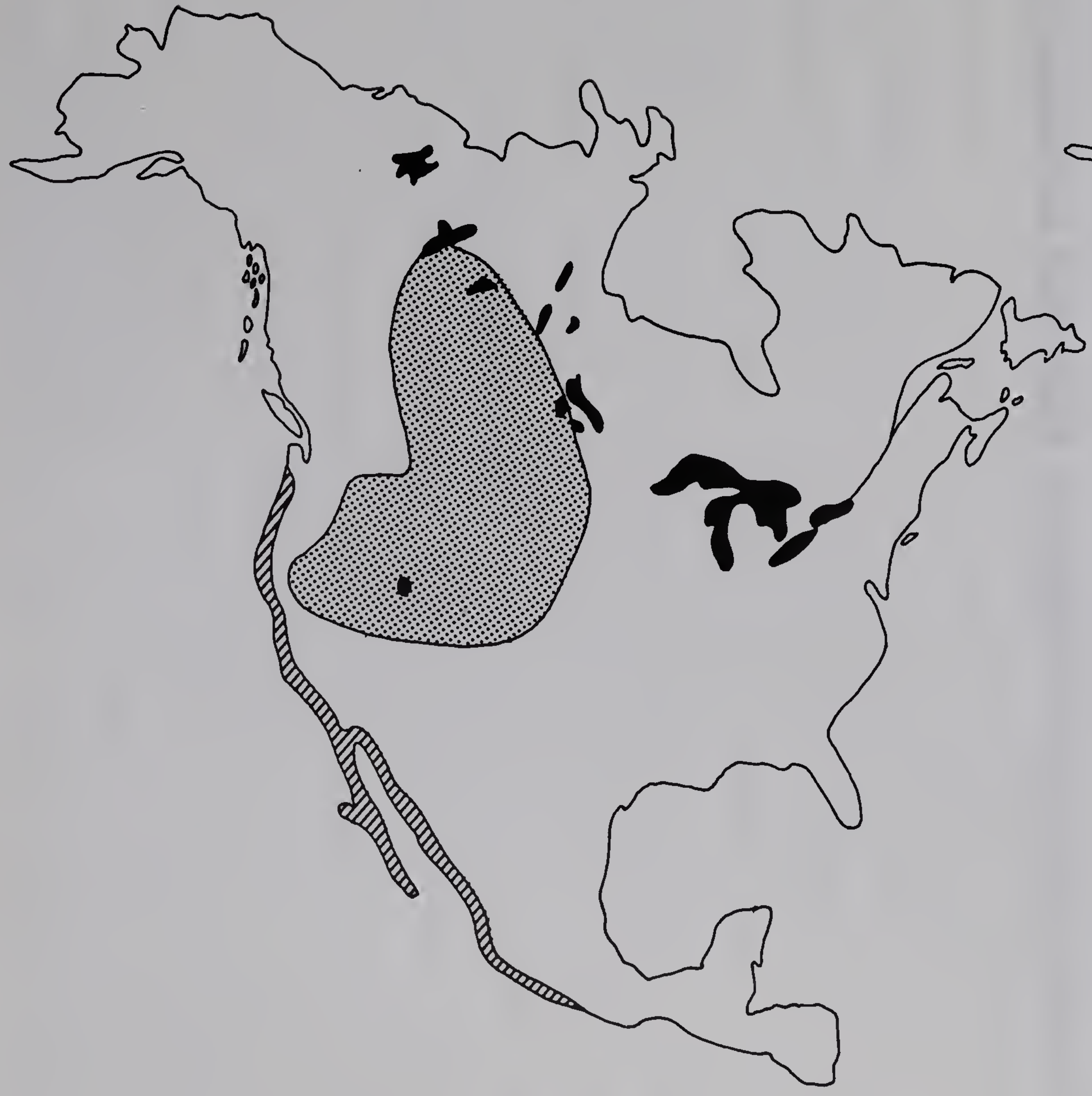
1. INTRODUCTION

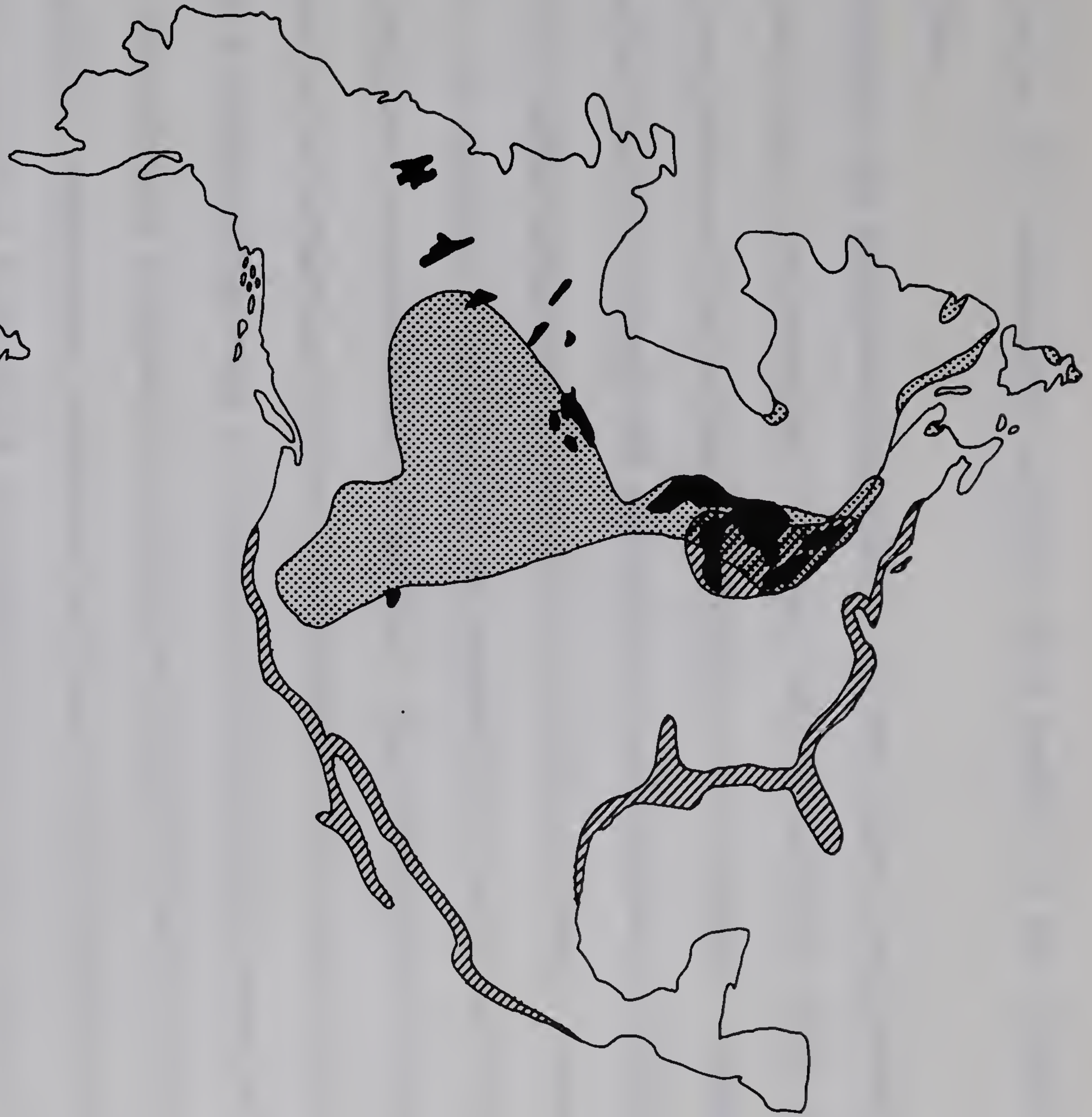
Fisher and Lockley (1954) state that the evolutionary radiation of gulls may have taken place from the North Pacific and Atlantic. They state that there are 42 species of gulls of which 16, 14, 11, 9, 6, 5 and 2 species are found in the North Pacific, North Atlantic, Arctic, South Pacific, Indian Ocean, South Atlantic and in the Antarctic, respectively.

Most studies of gulls have been conducted on coastal colonies (Coulson and White, 1956, 1958, 1959, 1960, 1961; Drost et al., 1961; Goethe, 1937, 1953, 1955, 1956, 1960; Harris, 1964; Kruuk, 1964; Moynihan, 1955, 1956, 1962; Paludan, 1951; Patterson, 1965; Paynter, 1947, 1949; Tinbergen, 1953, 1959; Ytreberg, 1956, 1960), obscuring the fact that the inland freshwater habitat is also successfully exploited by this group. The objective of the present study was to determine whether the success of gulls in the inland environment depended on special adaptations in breeding biology as compared to those using the coastal environment. This general problem was approached through a study of the California Gull (_Larus californicus_) and Ring-billed Gull (_L. delawarensis_) at Miquelon Lake (lat. 53° 15'N; long. 112° 55'W), Alberta. The California Gull is restricted to inland sites for breeding, and the Ring-billed Gull is an inland breeder with the exception of a small eastern section of its range (Fig. 1). Why these forms migrate from coastal wintering grounds to nest inland is a matter for speculation. Serventy (1960) suggested that the two chief factors governing the breeding distribution of sea-birds are 1) the occurrence or availability of food and 2) the presence of nesting sites. The mass movements of the California and Ring-billed Gulls may be interpreted as

Fig. 1 Breeding and winter ranges of California and Ring-billed Gulls (From A.O.U. Checklist, 1957 and Godfrey, 1966)



CALIFORNIA GULL



RING - BILLED GULL

▨ MAIN WINTER RANGE

▒ BREEDING RANGE

an exploitation of a seasonally abundant food supply in the interior of North America.

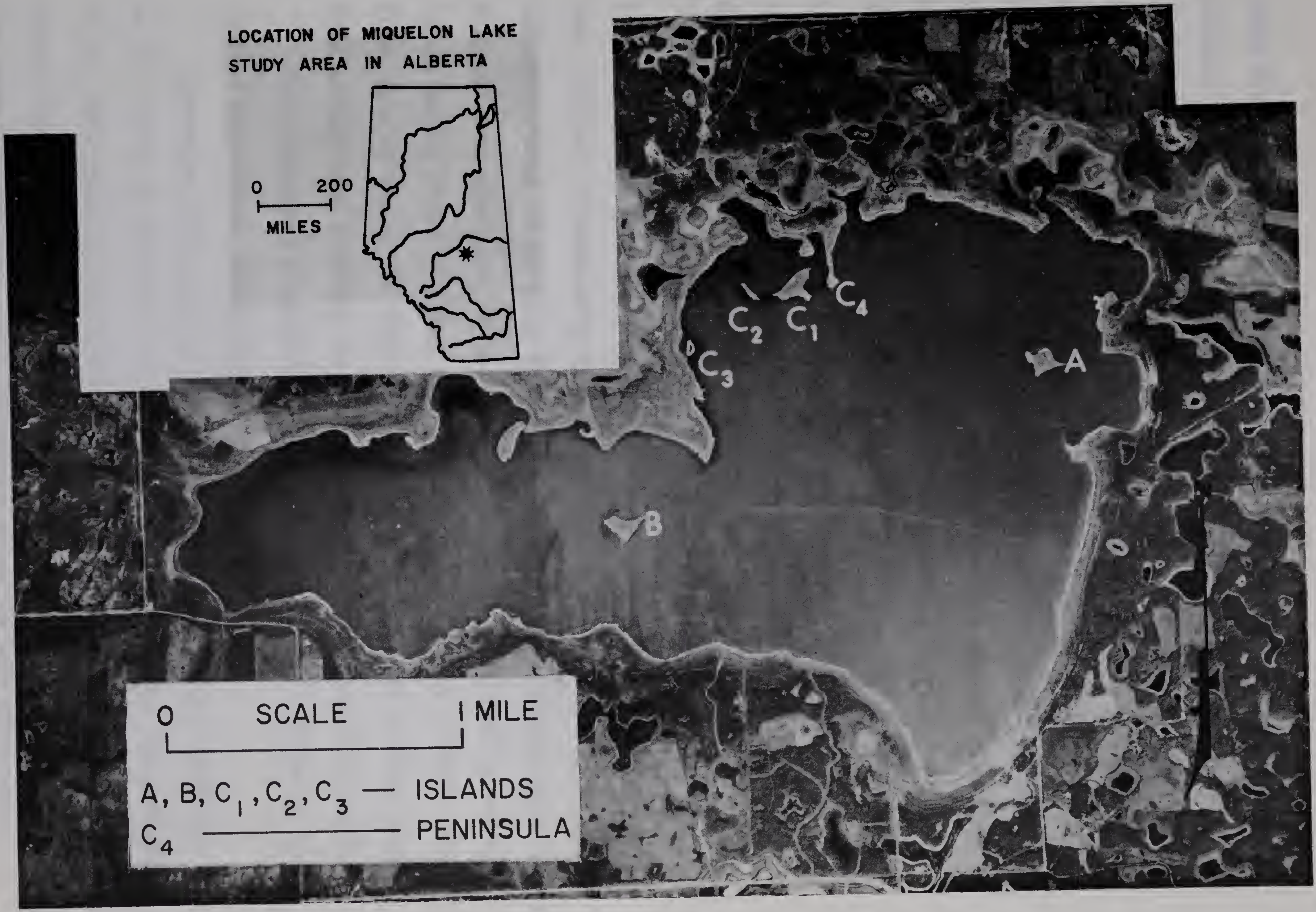
To discover the possible adaptations to the inland environment, breeding chronology, reproductive success, nesting habitat, food, helminth fauna and the growth of the chicks to fledging were studied. Studies of coastal gulls from the literature and from my own studies on Glaucous-winged Gulls, *Larus glaucescens*, in British Columbia formed a basis for comparison. In addition, California and Ring-billed Gulls nest together at many locations in western North America. The interaction of the species was studied, with particular emphasis on whether one species adversely affected the reproductive rate of the other as has been demonstrated between related gulls nesting together in coastal situations (Harris, 1964; Paludan, 1951). Particular attention was paid to anti-predator mechanisms, especially insofar as they might be unique to the inland situation.

2. METHODS

Procedure in the colony. This study was conducted at Miquelon Lake, 30 miles S.E. of Edmonton (lat. 53° 32'N; long. 113° 32'W), Alberta during the summers of 1964 and 1965. The California and Ring-billed Gulls nested on islands in Miquelon Lake. The same islands were inhabited in both years. Fig. 2 depicts Miquelon Lake and the position of the islands in the study area. A cabin was erected on island A in 1963 which served both as an observation tower and living quarters. Daily observations on the gull colonies were conducted from May 7 to August 8 on island A in 1964, and from April 23 to July 6 on islands A and B in 1965. The time of arrival, and dates of laying, hatching and fledging were recorded. Additional information on the time of arrival and departures of the gulls from the Edmonton area was obtained at such localities as garbage dumps.

The location of the gull nests and the species of the birds attending them were recorded. The nests of the two species could be recognized by differences in nest construction and egg sizes (Appendix 1). All gull nests were marked with sturdy wooden blocks, one foot long. These blocks were laid flat on the ground near the nest and thus could be placed in position quickly. Numbered metal tags were attached to them, providing the nests with a permanent nest number. The chronology of events during the reproductive cycles were recorded. The nests were checked daily from the time of my arrival in the spring until all the chicks had hatched. Checking was done as fast as possible, keeping movements known to disturb the gulls to a minimum. Nevertheless, gull predation on eggs in the laying period was increased by my activities. For this reason, nests in which eggs were lost, during the first days of the study, either through disappearance or

Fig. 2 Miquelon Lake



LOCATION OF MIQUELON LAKE
STUDY AREA IN ALBERTA
0
200
MILES
A
B
C$_1$
C$_2$
C$_3$
C$_4$
0 SCALE 1 MILE
A, B, C$_1$, C$_2$, C$_3$ — ISLANDS
C$_4$ — PENINSULA

being broken and eaten, were omitted from calculations of reproductive success. After three to four days the birds became accustomed to my presence in the colony and during incubation I could approach many nests within five feet before the incubating gulls would depart. Immediately after hatching, the young were marked with individual combinations of binders' tape on the legs. These were later replaced by individually numbered colored plastic bands and standard Wildlife Service aluminum bands. The fate of these marked chicks was followed through day to day searching of the study area. In 1965, the chronology of the breeding cycles of California Gulls and Ring-billed Gulls nesting on islands at the north end of Beaverhill Lake (22 miles from Miquelon Lake) was also investigated.

Since egg-laying was well advanced when the study began on island A in 1964 and on island B in 1965, the dates of clutch commencement were obtained by subtracting the average periods of egg-laying and incubation from the hatching dates. These periods were derived from clutches followed from egg-laying to hatching. I visited island B during the egg-laying period on May 7 and 11 in 1966 and on May 6 and 13 in 1967. The first date of laying for both species could be calculated in those years from average time intervals between the laying of the eggs of a clutch.

The behavioural interaction of the gull species was studied at the time of territorial establishment.

Vegetative cover and topography were analyzed and their influence on the choice of nest-sites of the gulls was investigated. The position of all gull nests on the islands at Miquelon Lake were plotted on maps of these islands. The distances between individual nests and between nests and the water were measured. Nest elevations above the lake level were estimated.

Food analysis. The food habits of both species were investigated in 1965 from adults collected in May, June and July and from chicks collected in the first week of July. Specimens were taken at Miquelon Lake and Beaverhill Lake. The contents of the esophagus and proventriculus were preserved. No differences were found between regurgitations and food obtained from the esophagi, so that samples from these sources were grouped for analyses. Gizzard contents were also analyzed. However, since certain foods in the gizzard are digested more rapidly than others, these results add nothing beyond showing that bias can occur if gizzards are the only organs investigated.

In addition to the sources of undigested food mentioned above, pellets, which represent the ejected masses of indigestible residues, were collected on the breeding grounds and analyzed separately. The gull species responsible was determined by where the pellets were found, a procedure involving little error in these spatially segregated colonies. Down feathers of gulls, grit and debris such as glass, paper, cloth, fruit pits, bottle caps, etc., were not taken into consideration.

The frequency of occurrence of specific food items was based on the number of occurrences of the item over the total number of esophagi and regurgitations. The volume of food was measured to the nearest cm^3 by submerging it in a graduated cylinder partially filled with water.

Growth. Gull chicks were weighed to the nearest gram on alternate days from hatching until fledging on island B in 1964. The chicks were weighed with a spring balance up to 150g, all subsequent readings were taken with a triple beam balance. The measurements were taken in a plot 300 feet by 100 feet fenced with a screen 2 feet high, in which both species were nesting.

Endoparasites. In order to assess the helminth fauna, 43 gulls of each species were collected on island B in Miquelon Lake in 1964. Of the 43 specimens of each species, 13 were adults and 30 were chicks. Eight adults were collected in the last week of May and five in the last week of June. The 30 chicks consisted of five groups of six chicks each in weekly age groups. An additional 44 adult gulls were collected in 1965 for helminth analyses. Eight adults of each species were collected in mid-May and eight of each in mid-June at Miquelon Lake. Five adult California and seven adult Ring-billed Gulls were collected in mid-July at Beaverhill Lake.

In 1965, two areas on island B at Miquelon Lake, each approximately 0.5 acres, containing 40 nests of each species were fenced to a height of two feet with chicken wire. The eggs from all California Gull nests were exchanged with those of Ring-billed Gull nests within the areas. The purpose of the exchange was to determine whether interspecific variation in the helminth fauna of the gulls resulted from a specific difference in susceptibility to helminths or from a specific difference in exposure to infective stages through dissimilar food habits. Twenty exchange chicks, ten from each area, were collected for helminth analysis when they were 21-23 days old in the first week of July. At the time that the foster chicks were collected, eight California and ten Ring-billed Gull chicks of similar age were taken for helminth analysis. These latter birds were collected at the Beaverhill Lake gull colonies, as no chicks of either species were available at Miquelon Lake apart from the foster chicks.

The gulls were frozen, then autopsied in the fall of the years in which they were collected. The helminths were fixed and stored in

AFA (alcohol-acetic acid-formaldehyde mixture). The cestodes were later stained with Ehrlich's hematoxylin and the trematodes with Chubb's hematoxylin.

Statistics and data from sources other than this study. Chi square tests of independence were used to test differences in extensity of helminth infection between gull species. The Clark-Evans method (1954) was used to test whether the observed nesting distributions of the gulls departed from random with respect to the distance to the nearest neighbor. In all statistical tests, the null hypothesis was accepted if the probability level was less than 0.05.

Reference made to the Glaucous-winged Gulls is in relation to my own findings on this species (Vermeer, 1963) unless otherwise stated.

3. DESCRIPTION OF THE STUDY AREA

Miquelon Lake is an alkaline body of water with a total alkalinity (in 1964) of 1383 ppm and a range in pH of 9.3 to 9.5 (Kerekes, 1965). At that time it was approximately 3 miles long by 2 wide and averaged 9 feet deep. Its muddy and sandy shores, which are strewn with pebbles and boulders, are generally free of emergent vegetation. Ridges of boulders and debris exist at various points along the shores and on the islands. These ridges have been created by wind-blown ice which grinds up on the shores at the time of spring break-up, pushing rock and debris in front of it. The ridges so formed were favoured by nesting California Gulls (Fig. 14).

The two main islands, A and B. (Fig. 2), on which the gull colonies were located, are composed of boulders, sand and clay, the latter mixed with decomposed vegetation. The main study area was island A. From comparison of aerial photographs taken in different years and from communication with a former resident in the area, it was learned that island A was exposed by the falling water level in the autumn of 1949. Island A had an area of approximately 6 acres in the spring of 1964 and was relatively flat, its highest point being 6 feet above the lake level. Island B had an area of approximately 5 acres in 1964 and its highest point was also 6 feet above the water level.

Vegetation. From comparison of the plant species on islands A and B with the flora of central Alberta, described by Moss (1959), the island vegetation seemed typical for insular situations in this region. In the summer and autumn, plant growth on the islands became luxurious, probably as the result of the fertilizing effect of the excrement of the nesting gulls. A few

small trees and shrubs, including *Populus tremuloides*, *Salix* sp., *Cornus stolonifera*, *Ribes oxyacanthoides* and *Rosa woodsii* grew on Island A. On Island B, there was only a small group of *Populus tremuloides* and a few *Ribes oxyacanthoides*. Along the peripheries of both islands there was a zone of *Glyceria striata* and *Hordeum jubatum*. *Suaeda depressa* grew on the muddy and sandy shore line, indicating the saline nature of the lake water (Moss, 1959). The most common herbs in the interior of the islands were *Urtica gracilis*, *Sonchus arvense*, *Artemisia absinthium*, *Descurainea richardsonii*, *Cirsium arvense*, *Chenopodium album*, *Scirpus americanus* *Scirpus validus*, *Axyris amaranthoides*, *Amaranthus retroflexus*, *Carex rostrata*, *Taraxacum officinale* and *Juncus balticus*. To a lesser extent were present *Chenopodium fremontii*, *Thlaspi arvense*, *Achillea millefolium*, *Potentilla anserina*, *Aster* sp., *Solidago decumbens*, *Galeopsis tetrahit*, *Trifolium pratense*, *Plantago major*, *Erigeron lonchophyllus*, *Convolvulus sepium*, *Bromus* sp., *Senecio vulgaris*, *Epilobium angustifolium*, *Agrimonia striata* and *Polygonum amphibium*. Only *Ruppia occidentalis* seemed to grow on the lake bottom.

Vertebrates.

Fish. Two species of fish were found in the lake, *Eucalia inconstans*, which was relatively common, and *Perca flavescens*, which was scarce (Kerekes, 1965).

Mammals. The mammalian species recorded on island A were: *Mustela rixosa*, *Sorex cinereus*, *Peromyscus maniculatus* and *Microtus pennsylvanicus*.

Birds. Table 1 shows the nests found on islands A and B in 1964 and 1965.

Table 1. Number of nests of birds found on islands A and B in 1964 and 1965

Species	Number of nests Island A 1964	 1965	 Island B 1964	 1965
California Gull (Larus californicus)	470	87	300*	44
Ring-billed Gull (Larus delawarensis)	315	58	1200*	378
Canada Goose (Branta canadensis)	0	0	1	1
Lesser Scaup (Aythya affinis)	41	44	26	32
Gadwall (Anas strepera)	26	15	3	10
Mallard (Anas platyrhynchos)	9	3	3	3
White-winged Scoter (Melanitta fusca)	9	2	2	7
Baldpate (Mareca americana)	3	1	2	1
Pintail (Anas acuta)	2	4	4	6
Common Tern (Sterna hirundo)	1	0	0	0
Marbled Godwit (Limosa fedoa)	1	0	0	0
Spotted Sandpiper (Actitus macularia)	0	1	0	0

* Estimations

One old nest of a Crow (Corvus brachyrhynchos) was found in a young Populus tremuloides on island A. Crows did not nest on the islands during the time of the field study, presumably because of my presence. Nests of Savannah Sparrows (Passerculus sandwichensis) were not found, but these birds probably bred there. If nesting, they were the only passerines breeding on islands A and B in 1964 and 1965.

Six California Gull nests were found in region C (Fig. 2) in 1964. Two of these were located on peninsula C4. In 1965, 65 pairs of California Gulls nested in region C. Common Terns also nested in region C. Birds

found breeding in association with them were Avocets (*Recurvirostra americana*), Wilson Phalaropes (*Steganopus tricolor*), Piping Plovers (*Charadrius melodius*), Pintails, Baldpates and Lesser Scaup.

Other waders and waterfowl which nested along the shore of Miquelon Lake were Killdeer (*Charadrius vociferus*), Willets (*Catoptrophorus semipalmatus*), Red-necked Grebes (*Podiceps grisegena*), Mallards, Gadwalls, Pintails, Blue-winged Teals (*Anas discors*) Lesser Scaup, Shovelers *Spatula clypeata*) and Redheads (*Aythya americana*).

4. THE BREEDING SCHEDULE: CHRONOLOGY

4.1 Migration Fig. 3 depicts the winter recoveries of juveniles* raised at Miquelon Lake in 1964. It can be seen that the juveniles of both species have the same winter range, chiefly southern California and the west coast of Mexico. Farley (1932) found that the California and Ring-billed Gulls raised at Bittern Lake, 15 miles from Miquelon Lake, also winter mainly in southern California. Although the Ring-billed Gull is a common fall migrant at Vancouver, British Columbia, it is rarely observed there in the spring. The California Gull by contrast, is numerous in both fall and spring. From the observations cited by Houston (1963), it appears that the California Gulls migrate along the West Coast, north in the spring from California to southern British Columbia and then inland to the interior; in the fall they presumably migrate the reverse route southward. The Ring-billed Gulls, however, more commonly migrate north through the interior of the continent.

The first white-headed gulls (California or Ring-billed Gulls, but definitely Ring-billed Gulls in 1967) were observed in the Edmonton area on March 29, 1964, March 30, 1965, March 28, 1966 and April 2, 1967 by R. Lister, J. C. Holmes, D. Newman and R. Lister respectively (pers. comm.). In the first week of April in those four years I observed only Ring-billed Gulls in the Edmonton area.

The change of daylength, because of its precision, seems to be used

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* The term "juvenile" denotes a fledged gull, from the same season, which has left the nesting colony. A "fledgling" denotes a gull which has fledged but has not left the nesting colony.

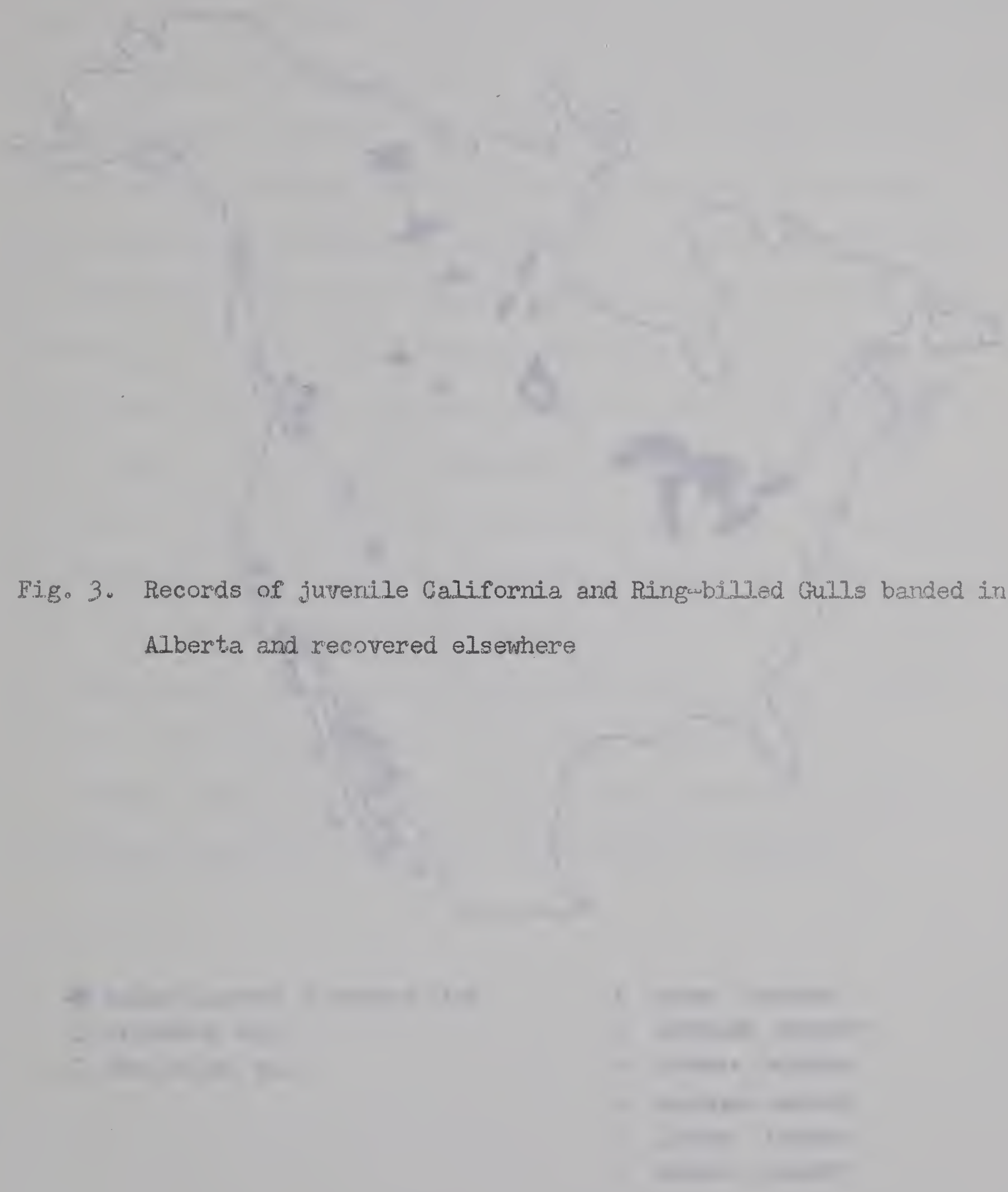
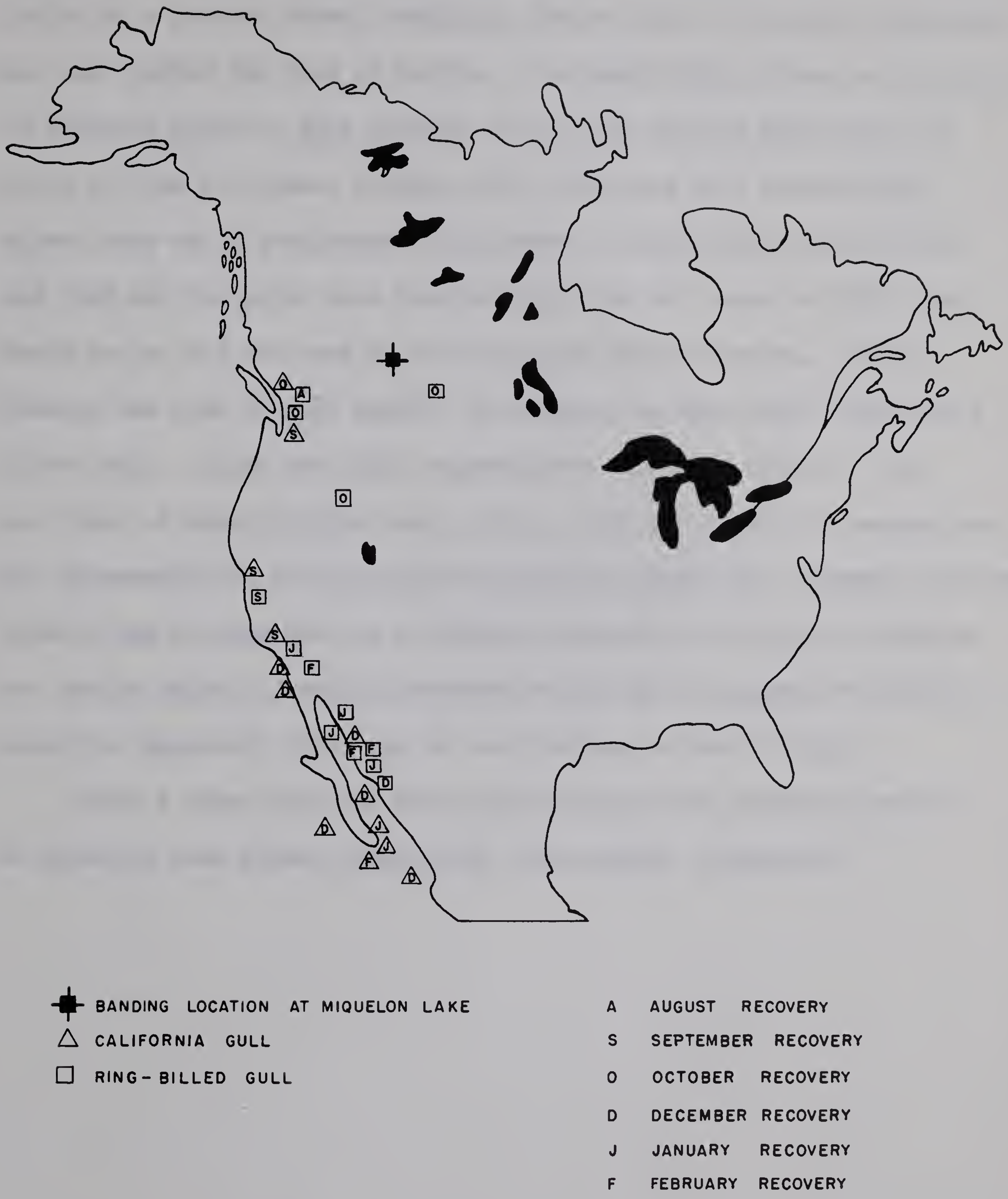


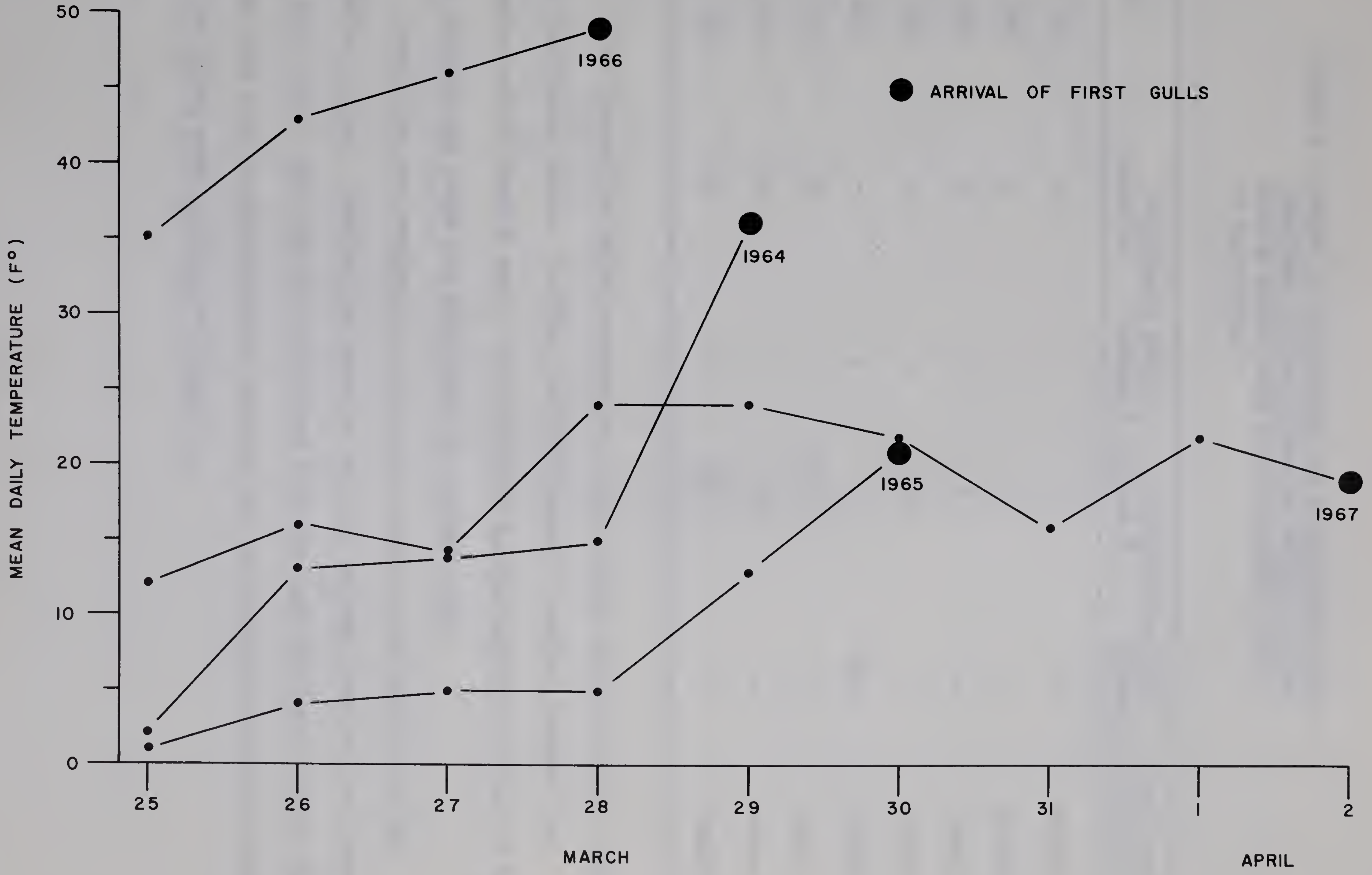
Fig. 3. Records of juvenile California and Ring-billed Gulls banded in Alberta and recovered elsewhere


BANDING LOCATION AT MIQUELON LAKE
△ CALIFORNIA GULL
☐ RING-BILLED GULL
A AUGUST RECOVERY
S SEPTEMBER RECOVERY
O OCTOBER RECOVERY
D DECEMBER RECOVERY
J JANUARY RECOVERY
F FEBRUARY RECOVERY

in the timing of arrival by many mid-and high latitude migratory birds (Farner, 1964; Wolfson, 1960). Besides the increasing daily photoperiod as a primary timer, modifying factors such as climatic conditions may also govern the time of arrival. The mean depth of snow on the ground in Edmonton prior to gull arrival in the last week of March was 1.8, 11.0, 3.3 and 9.6 inches in 1964, 1965, 1966 and 1967 respectively. Since there was a considerable difference in snow depth between 1964 and 1965 and the gulls were observed only one day later in 1965, snow depth per se did not seem to influence the time of arrival. Fig. 4 relates the time of gull arrival in Edmonton to mean daily temperature in the city. Since the daily temperatures were much higher in the last week of March in 1966 than in 1964, 1965 and 1967, air temperature was apparently not the only factor affecting migration. However, air temperature may be important as a threshold factor; that is, the birds may not arrive unless a certain temperature has been surpassed at points along the migratory route and at the terminus of their flight.

Table 2 shows that the first gulls reached the breeding grounds at Miquelon Lake almost immediately upon arrival in Edmonton.

Fig. 4. Observed arrival of the first white-headed gulls (Ring-billed Gulls?) in relation to mean daily temperature in the Edmonton area. (From monthly meteorological summaries at Edmonton city, Alberta).


50
40
30
20
10
0
MEAN DAILY TEMPERATURE (F°)
25
26
27
28
29
30
31
1
2
MARCH
APRIL
1966
1964
1965
1967
● ARRIVAL OF FIRST GULLS

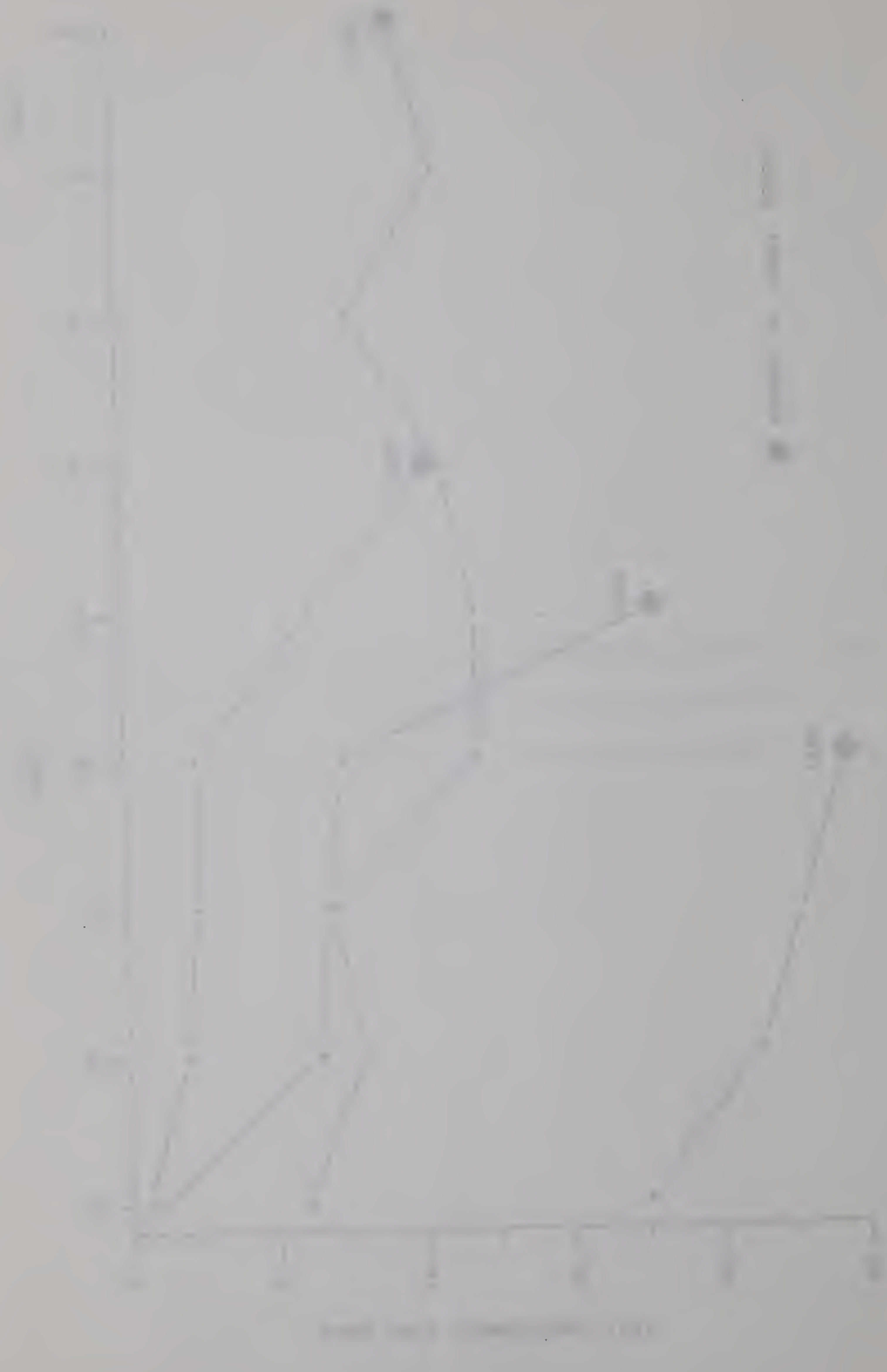


Table 2. Number of California and Ring-billed Gulls observed on the islands at Miquelon Lake during visits made by the observer prior to egg-laying

Date	California Gull		Ring-billed Gull		Snow conditions on islands
	Island A	Island B	Island A	Island B	
March 30, 1964	0	-	3	-	Present
April 2, 1966	0	-	3	-	Present
April 3, 1965	0	-	1	-	Present
April 4, 1965	0	-	2	-	Present
April 8, 1966	-	0	-	120	Present
April 12, 1964	10	-	190	-	Absent
April 21, 1966	30	-	70	-	Absent
April 23, 1965	80	-	120	-	Present

The Ring-billed Gulls returned to their nesting habitat earlier than the California Gulls. In 1966, the difference in arrival between the species was at least a week. The different spring migratory routes of the two species may cause the difference in arrival time.

Some data are available on the autumn migration of gulls from the Edmonton area. Observations made at the city garbage dump in the autumns of 1963, 1964, 1965 and 1966 indicated that the last California Gulls departed from this site in mid-September, whereas the last Ring-billed Gulls departed in the first week in November (Table 3).

Table 3. Autumn observations of the numbers of California and Ring-billed Gulls at the city garbage dump in Edmonton

Date	No. of birds seen	
	California Gull	Ring-billed Gull
August 15, 1964	ca. 500	ca. 1000
August 29, 1966	10	190
Sept. 6, 1965	4	ca. 500
Sept. 18, 1964	0	ca. 500
Sept. 18, 1966	2	155
Oct. 16, 1966	0	ca. 500
Oct. 30, 1963	0	ca. 400
Nov. 3, 1964	0	100
Nov. 6, 1963	0	6
Nov. 7, 1964	0	0
Nov. 8, 1965	0	0
Nov. 10, 1964	0	0

4.2 Colony occupation The gulls occupied the islands in Miquelon Lake before snow and ice disappeared (Table 2). In 1964, 1965 and 1966, the ice disappeared from Miquelon Lake on April 30, May 8 and May 7, respectively. Snow disappeared from the islands on April 12 in 1964, on April 30 in 1965 and sometime in the second week of April in 1966. The first Ring-billed Gulls arrived in the beginning of the first week of April and the California Gulls in the second week of April.

Where spring arrives sooner at more southern latitudes, the California Gulls arrive earlier on the breeding grounds. Behle (1958) states that the California Gulls arrived at Great Salt Lake in Utah in late February and Rothweiler (1960) reports that they arrived on March 12 in 1959 at Freezout Lake, Montana. Besides arriving earlier, they commenced laying before the California Gulls at Miquelon Lake. The California Gulls started laying about the second week of April in Utah (Behle, 1958), and on April 22, 1959 at Freezout Lake, Montana (Rothweiler, 1960).

In Table 4, the pre-egg periods of the gulls at Miquelon Lake are compared with those of the California Gulls in Montana and Utah and with that of the coastal Glaucous-winged Gull on Mandarte Island. The pre-egg period is considered to be the time between the appearance of the first individuals of a species on the breeding grounds and the laying of their first egg.

Table 4. Pre-egg periods of three species of gulls

Species	Pre-egg periods in weeks	Location and year of study	Authority source
Glaucous-winged Gull	10-12	Mandarte Island, British Columbia, 1961, 1962	Vermeer, 1963
California Gull	6-7	Great Salt Lake, Utah, several decades	Behle, 1958
California Gull	6-7	Freezout Lake, Montana, 1958, 1959	Rothweiler, 1960
California Gull	3-4	Miquelon Lake, Alberta, 1964, 1965	This study
Ring-billed Gull	4-5	Miquelon Lake, Alberta, 1964, 1965	This study

It can be seen that the California Gulls in Montana and Utah have a longer pre-egg period than the gulls at Miquelon Lake, but the former still have a much shorter pre-egg period than that of the coastal Glaucous-winged Gulls at Mandarte Island. Short pre-egg periods seem to be associated with more northerly gull populations and with the less hospitable conditions of the inland environment as compared to that of the marine habitat.

Although the Ring-billed Gulls arrived at Miquelon at similar dates in three years (the exact dates of the arrival of the California Gulls are not known), the first appearance of the gulls on the breeding grounds may vary annually. Paludan (1951) found that the occupation of the colony by Herring Gulls (L. argentatus) on Graesholm Island in the Baltic may be delayed for a month by unusually low temperatures and by dull weather. Ytreberg (1956), in three years of observation, recorded a two-week

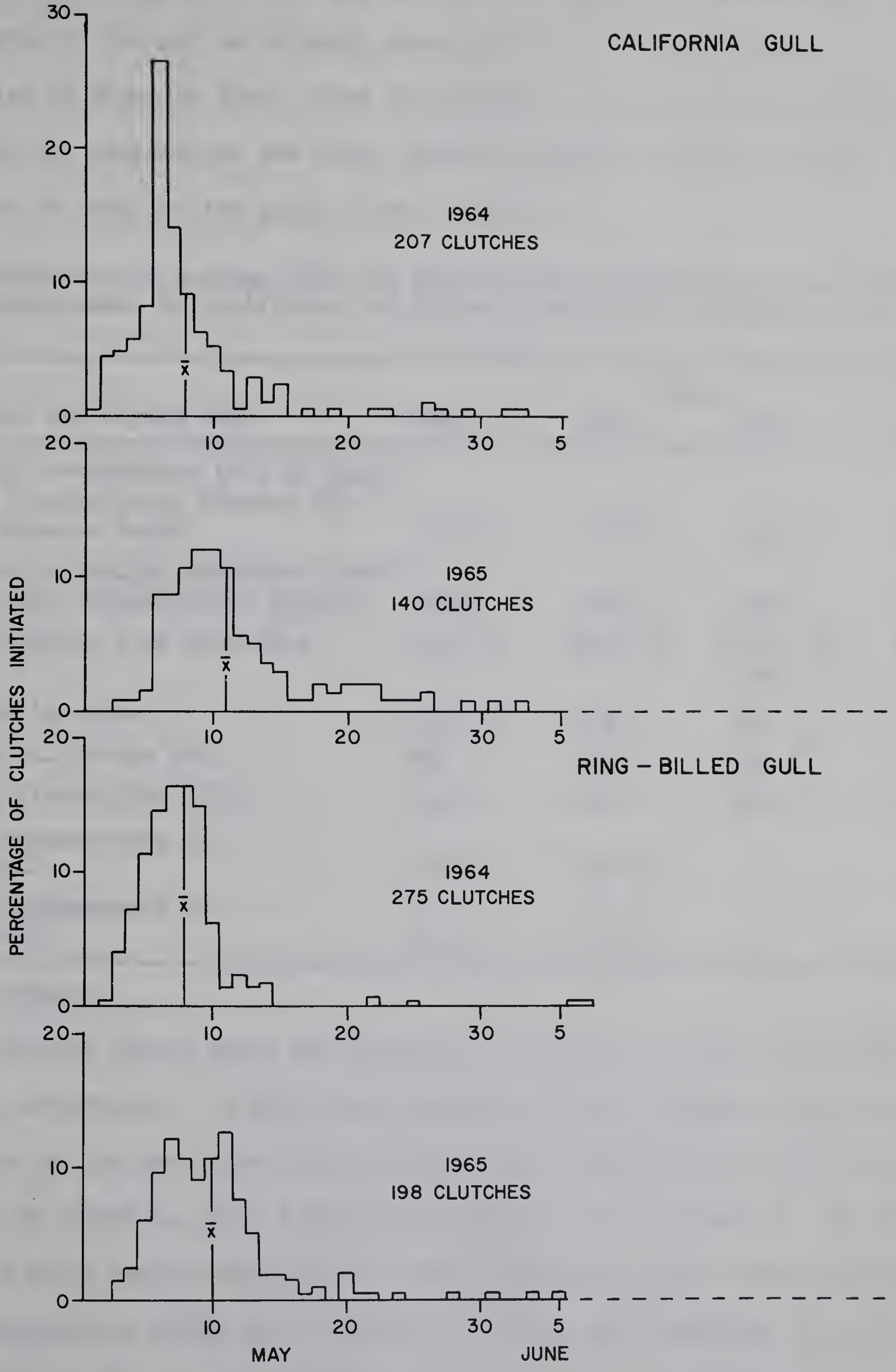
difference of the Black-headed Gull's (L. ridibundus) occupation of the colony situated on the outer edge of a vegetation belt on a lake near Oslo, Norway. The Black-headed Gulls did not occupy the colony until all that remained of the ice was a large perforated sheet. Ytreberg states that the late melting of ice delayed the occupation of the colony by the birds. According to Bergman (1939) the times of the colony occupation by the Herring Gull and the Mew Gull (L. canus) on islands in the Baltic are also dependent upon the melting of the ice. Since the California Gulls and Ring-billed Gulls at Miquelon Lake arrived long before the ice thawed, their occupancy does not depend on the melting of the ice. The coastal gulls may depend to a greater extent upon the availability of an aquatic food supply, which is not available until after the ice melts.

When I occupied island A on April 23 in 1965, the island was completely covered with snow. The initial courtship and territorial activities of the gulls occurred on this snow cover and was limited to two periods a day. The main activity occurred shortly after the gulls arrived at the island near dawn (0400 hours). Most of the birds left after 0900 hours. At 1700 hours they started to arrive again and a lower peak of activity occurred. At sunset (2000) hours all gulls left the island for roosting places. The gulls did not remain on the island during the night until laying had started. A similar daily rhythm was observed during the pre-egg period in the Glaucous-winged Gulls on Mandarte Island.

One of the large roosting places where California and Ring-billed Gulls were observed to spend the night was on Big Lake (4 miles from Miquelon Lake) near Edmonton. Tinbergen et al. (1962) argued that roosting on wide open mud flats and beaches might protect adult gulls against predation. Kruuk (1964) collected data on 1449 adult Black-headed Gulls killed by foxes and his data confirm that they are safe when roosting on open beaches, except on extremely dark nights. On the other hand, they were preyed upon to a considerable extent while roosting on the breeding grounds. The absence of adult gulls from the breeding colony at night during the pre-egg period may reduce predator facilitation.

4.3 Clutch commencement. Fig. 5 depicts the clutch commencement in 207 California and 275 Ring-billed Gull nests on island A in 1964 and that of 140 California and 198 Ring-billed Gulls on islands A and B in 1965. In 1965, the mean dates of clutch commencement for the California and Ring-billed Gulls were respectively 3.7 and 2.4 days later than for those species in 1964. The differences in the mean date of clutch commencement between the years were statistically significant for each species. The earlier laying in 1964 than in 1965 (and also 1966) may have been the result of more favourable weather. In Table 5, weather data are compared with the date of laying of the first egg and the mean date of clutch commencement in California and Ring-billed Gulls. Laying is delayed with a decrease in mean monthly air temperatures. Kirkman (1937) also found a correlation between low temperatures and late laying in the Black-headed Gulls in England. However, Bergman (1939) stated that

Fig. 5. Distribution of clutch initiation of California and Ring-billed Gulls at Miquelon Lake.


CALIFORNIA GULL
1964
207 CLUTCHES
1965
140 CLUTCHES
RING – BILLED GULL
1964
275 CLUTCHES
1965
198 CLUTCHES
PERCENTAGE OF CLUTCHES INITIATED
30
20
10
0
x̄
10
20
30
5
MAY
JUNE

the start of laying in Herring and Mew Gulls in Finland is dependent upon the melting of the ice and not directly upon the temperature. The presence of ice per se probably does not delay laying in the two species at Miquelon Lake, since the melting of the ice is a function of the air temperature and since aquatic organisms are not a major source of food for the gulls in May (section 7).

Table 5. Comparison of weather data and dates of the first egg and mean clutch commencement in California and Ring-billed Gulls at Miquelon Lake

Weather and laying data	Year 1964	1965	1966	1967
Mean daily air temperature (°F) in April at Edmonton International Airport (25 miles from Miquelon Lake)	39.0°	35.2°	32.6°	29.2°
Total duration of bright sunshine (hours) in April at Edm. International Airport	232.9	209.1	213.7	237.7
Islands in Miquelon Lake snow free	April 12	April 30	April 2nd week	May 2
Miquelon Lake ice free	April 30	May 8	May 7	May 17
First egg of California Gull	May 1	May 3	May 9*	May 11*
First egg of Ring-billed Gull	May 2	May 3	May 4	May 8
Mean clutch commencement in California Gull	May 8	May 11	-	-
Mean clutch commencement in Ring-billed Gull	May 8	May 10	-	-

* Few gulls present

Another factor which may influence the time of clutch commencement is human disturbance. In 1965, the California Gulls commenced laying on both islands at the same time, but the Ring-billed Gull started to lay five days later on island A, where I had been working, than on island B. The Ring-billed Gulls began nesting while I was temporarily absent from the island. The Ring-billed Gulls were observed to be much more excitable than the California Gulls, and my residence on island A may have caused the later start of laying in the Ring-billed Gulls on that island.

The appearance of food per se did not appear to be a primary factor

in the onset of egg-laying of the gulls. Although an abundance of voles (Microtus pennsylvanicus) and snow-free conditions provided abundant food in mid-April, 1966, at least three weeks earlier than in the previous year, laying did not begin earlier. Belopolskii (1957) interpreted regional difference in the onset of laying in sea birds in the Barents Sea as evidence that changing daylength was not the factor determining the time of laying. He stated that food was responsible for the initiation of the breeding cycle. However, the influence of light and the effect of food on the time of egg-laying in birds are not mutually exclusive. Changing daylength not only stimulates the birds' sexual cycle, but also governs the increase of food at high latitudes. In regions closer to the equator, where seasonal light changes are not pronounced and therefore may not be important in controlling food sources to the same extent as in northern regions, food may be the principal timer in the onset of breeding. Kahl (1964) reported that the breeding of Wood Storks (Mycteria americana) in Florida closely coincided with food availability as influenced by declining water levels.

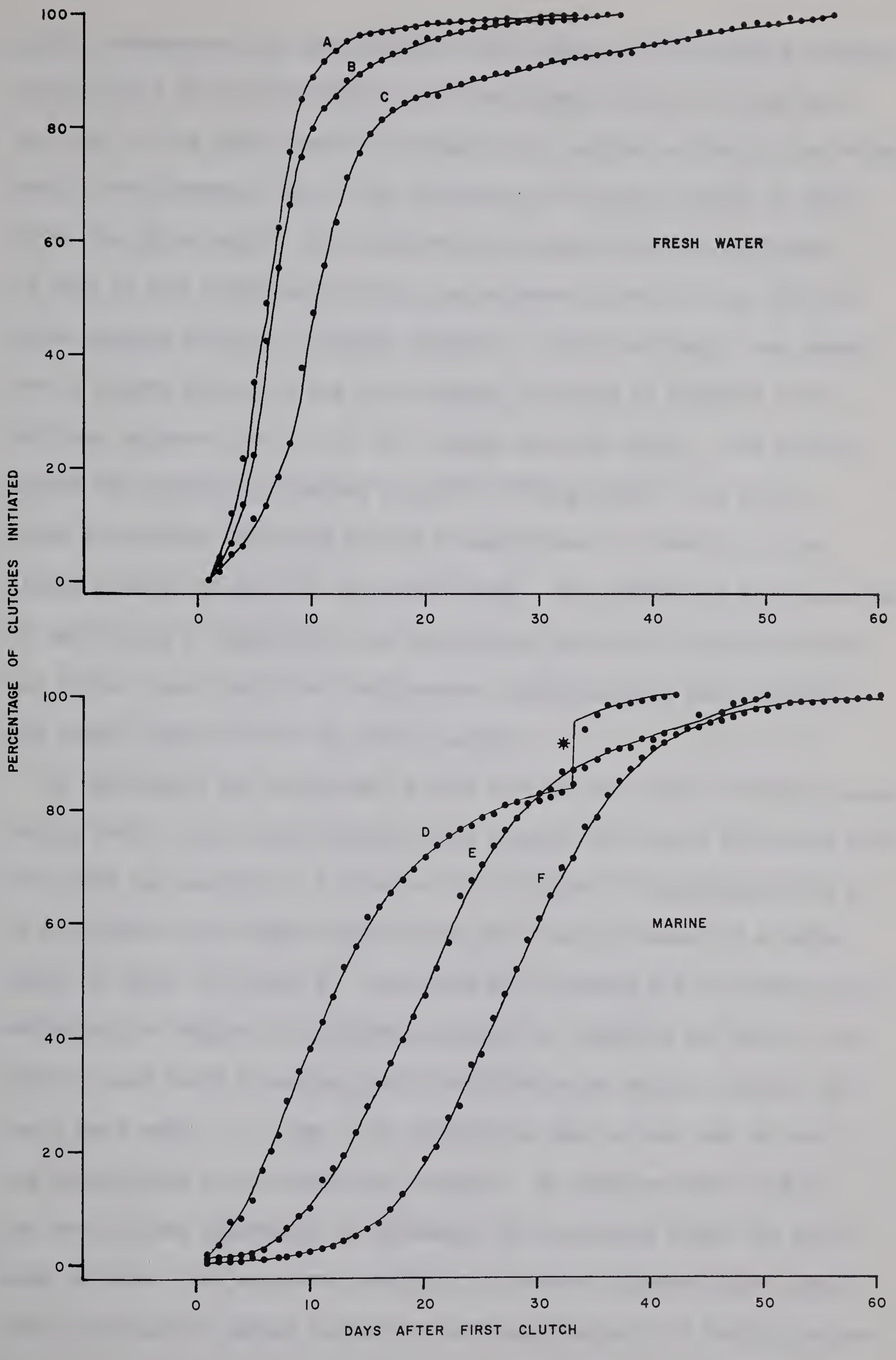
In Fig. 6, the concentration and duration of clutch initiation of California and Ring-billed Gulls at Miquelon Lake is compared with that of Herring and Lesser Black-backed Gulls (Larus fuscus) on Graesholm Island in the Baltic Sea (Paludan, 1951), Black-headed Gulls on a fresh water body near Oslo, Norway (Ytreberg, 1956) and Glaucous-winged Gulls nesting on Mandarte Island. The graph for each species is based on clutch commencements in two successive annual laying seasons. It is evident that clutch initiation in California and Ring-billed Gulls is concentrated at the start of the laying season, while that in the three species nesting on marine islands is more normally distributed throughout the laying period.

Fig. 6. Cumulative distribution of clutch initiation in six gull species

Freshwater:
- A. Ring-billed Gull (This study)
  53°15'N, inland, 473 clutches
- B. California Gull (This study)
  53°15'N, inland, 347 clutches
- C. Black-headed Gull (Ytreberg, 1956)
  59°55'N, coastal, 363 clutches

Marine:
- D. Herring Gull (Paludan, 1951)
  55°18'N, coastal, 214 clutches
- E. Lesser Black-backed Gull (Paludan, 1951)
  55°18'N, coastal, 273 clutches
- F. Glaucous-winged Gull (Vermeer, 1963)
  48°38'N, coastal, 792 clutches

* Large number of replacement clutches started after a snowstorm


100
80
60
40
20
0
0
10
20
30
40
50
60
A
B
C
FRESH WATER
PERCENTAGE OF CLUTCHES INITIATED
100
80
60
40
20
0
0
10
20
30
40
50
60
D
E
F
✱
MARINE
DAYS AFTER FIRST CLUTCH

Clutch commencement in Black-headed Gulls takes an intermediate position between that of the California and Ring-billed Gulls on the one hand and that of the three species nesting in the marine habitat on the other hand. For instance, 80% of the clutches were started within 10 days after the first egg by the California and Ring-billed Gulls, within 15 days by the Black-headed Gulls and between 25 and 35 days for the three species nesting on marine islands. Clutch initiation was spread over a longer period in the four species breeding in habitats with a maritime climate than in the two species nesting inalnd. The greater degree of synchrony of laying in gulls nesting inland than at the coast at similar latitudes may be an adaptation to breeding in the inland habitat as will be discussed later. The effects of this synchrony of egg-laying in California and Ring-billed Gulls are that practically all chicks reach peak food requirements simultaneously when insects, the staple June diet of the gulls, abound.

An experiment was conducted in 1964 to test the extent to which repeat laying could occur, when clutches were removed four weeks after the date the first egg was laid. A total of 154 clutches of Ring-billed and 63 of California Gulls were taken on May 28, from the centre of a dense group of nests on island B. The nests were checked the following day to determine the degree of disturbance caused by removing the eggs. Both species were found occupying their territories as usual, although the nests were empty. On June 3 one California Gull clutch and on June 4 one Ring-billed Gull clutch were started. No clutches were laid in the area of the experiment or elsewhere in the colony after the first week of June. The apparent inability to produce clutches three weeks after the peak of laying appears to be characteristic of California and

Ring-billed Gulls. Black-headed Gulls in Norway (Ytreberg, 1956) and Glaucous-winged Gulls in British Columbia could readily renest, even as late as three weeks and one month, respectively, after the first hatching occurred. The apparent anomaly showing in the cumulative distribution curve of clutch initiation in the Herring Gulls in Fig. 6 was caused by a snowstorm which destroyed 35 clutches of the Herring Gulls 22 days after egg-laying started. Eighty-five per cent of these clutches were replaced 11 to 12 days later.

4.4 Hatching. Fig. 7 depicts the commencement of hatching in both gull species. The dates of hatching are based on the emergence of the first chick in each clutch. The mean dates on which California Gull chicks commenced hatching fell on June 6 in 1964 and June 13 in 1965. Those of the Ring-billed Gull fell on June 4 in 1964 and June 14 in 1965. In 1964, the Ring-billed Gull chicks hatched on the average 1.7 days earlier than the California Gull chicks. The difference in the mean date of hatching between the species in 1964 was statistically significant. The later hatching of the California Gull chicks resulted from the significantly longer incubation period in this species than in the Ring-billed Gulls (Table 6). That the hatching periods of the California and Ring-billed Gulls did not differ more than 1.7 days resulted from the similar laying periods of the two species.

Fig. 7. Distribution of the initiation of hatching of California and Ring-billed Gulls at Miquelon Lake

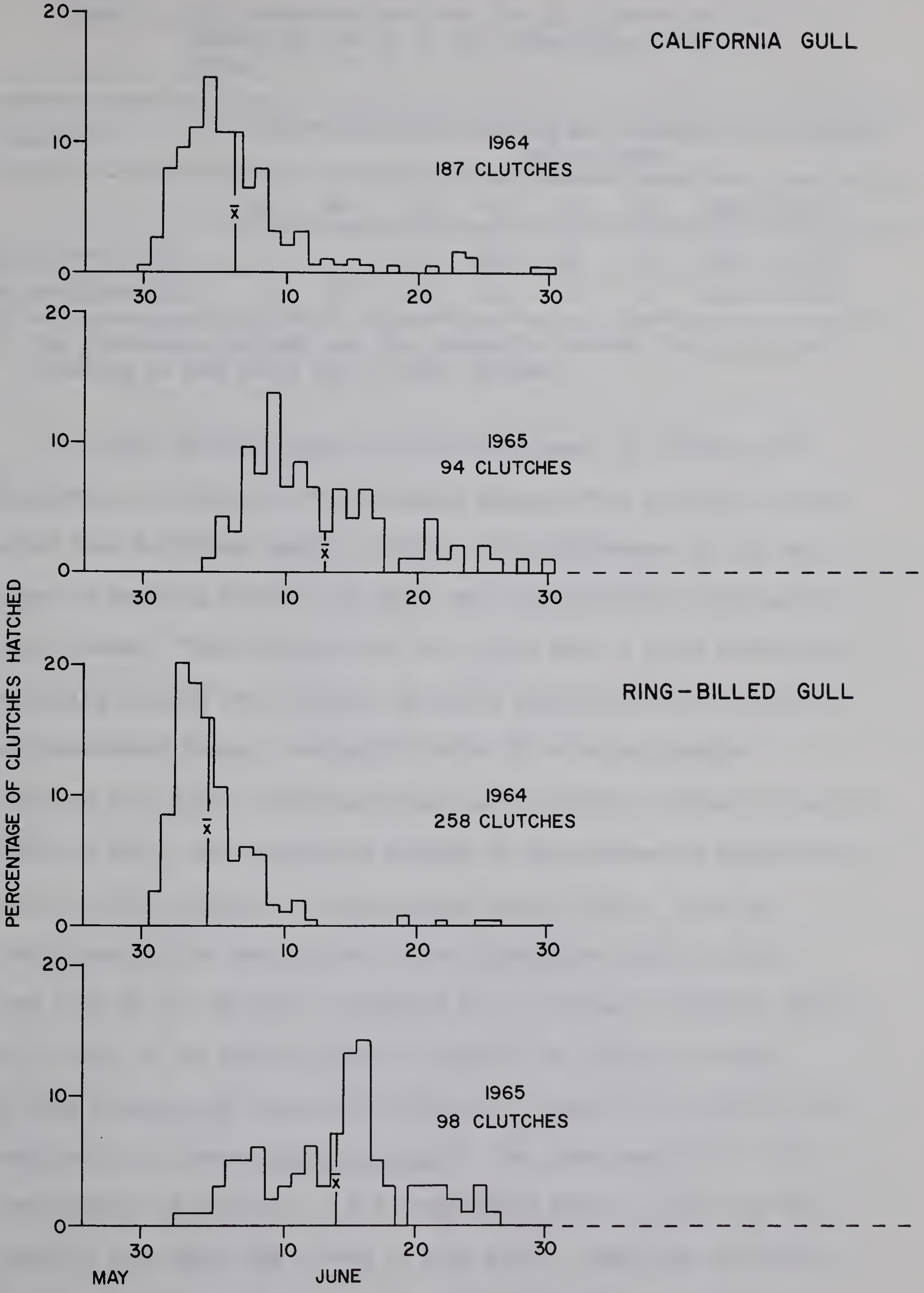

CALIFORNIA GULL
1964
187 CLUTCHES
1965
94 CLUTCHES
RING-BILLED GULL
1964
258 CLUTCHES
1965
98 CLUTCHES
PERCENTAGE OF CLUTCHES HATCHED
20
10
0
30
10
20
30
x̄
MAY
JUNE

Table 6. The incubation periods* for 57 clutches of the California and 64 of the Ring-billed Gulls in 1964.

Species	Intervals between laying and hatching of the third egg in days						
	23	24	25	26	27	28	Mean ± SE
California Gull			3	22	29	3	26.6 ± 0.09
Ring-billed Gull	1	17	33	11	1	1	25.0 ± 0.10

* The incubation periods are the intervals between the laying and hatching of the third egg of each species.

In 1965, the mean dates of the commencement of hatching for California and Ring-billed Gulls were respectively 6.5 and 9.7 days later than for those species in 1964. The differences in the mean dates of hatching between the years was statistically significant in each species. These differences are linked with a later commencement of laying in 1965 and possibly increased human disturbance as well as disturbance through nocturnal visits of an avian predator (section 5). These disturbances may have prolonged incubation in the gulls in 1965. The incubation periods of 20 clutches of California Gulls in 1965 averaged 2.8 days longer than in 1964. Only two incubation periods were known in the Ring-billed Gulls in 1965. They were 28 and 29 days as compared to an average incubation period of 25 days in the previous year. Emlen et al. (1966) reported delayed hatching in Ring-billed Gulls as a result of nocturnal disturbance by a raccoon (Procyon lotor). The late mean date of the commencement of hatching in the Ring-billed Gulls in 1965 may have resulted from early egg losses in that year. These egg losses may be linked to a snowstorm occurring during incubation as will be discussed later.

Since egg-laying was observed to be highly synchronized in the California and Ring-billed Gulls, incubation in those species could possibly become effective earlier than for gulls nesting in a coastal habitat. For this reason, the amount of effectual incubation applied to the eggs during the laying period was calculated from differences in known time intervals in laying versus those in hatching between successive eggs of a clutch (Table 7).

Table 7. Intervals between the laying and hatching of successive eggs in clutches of California and Ring-billed Gulls in 1964.

Species	California Gull								Ring-billed Gull							
Eggs:	I - II egg				II - III egg				I - II egg				II - III egg			
Intervals in days	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3
Number of laying intervals		2	14	1		1	10	2		4	15	2		4	21	2
Number of hatching intervals	17	17			3	20	5		39	29	1		9	53	11	1
Mean ± SE of laying intervals	1.94 ± 0.10				2.08 ± 0.14				1.90 ± 0.12				1.93 ± 0.09			
Mean ± SE of hatching intervals	0.50 ± 0.08				1.07 ± 0.10				0.53 ± 0.06				1.05 ± 0.06			

It is evident that the hatching intervals are shorter than the laying intervals. Therefore it can be deduced that incubation does not become fully effective during the laying period. Incubation becomes fully effective at the time when the maximum brood-patch temperature is applied to the eggs, which takes place approximately a week after clutch completion in the Herring Gulls (R. H. Drent, pers. comm.). The amount of effectual incubation applied to the eggs during the laying period was calculated with the following formula and expressed as a per cent:

$$\text{Incubation effectiveness} = \frac{\text{Time interval between the hatching of successive eggs in a clutch}}{\text{Time interval between the laying of successive eggs in a clutch}} \times 100$$

For the California Gulls, I calculated that only 26% and 51% of the full incubation effectiveness was achieved after the first and second egg, respectively. The corresponding figures for the Ring-billed Gulls were 28% and 54%. The percentage incubation effectiveness during laying in the inland breeding California and Ring-billed Gulls is compared with that of four species of gulls breeding along the marine coasts in Table 8. It can be seen that the effectiveness of incubation during the laying period is similar in the two groups of gulls.

Table 8. Comparison of effectiveness of incubation during laying in six species of gulls

Gull species	Percentage incubation effectiveness Interval between first and second egg	Interval between second and third egg	Authority
Herring Gull	30	53	Paludan, 1951
Lesser Black-backed Gull	18	60	Paludan, 1951
Black-headed Gull	28	52	Ytreberg, 1956
Glaucous-winged Gull	31	53	Vermeer, 1963
California Gull	26	51	This study
Ring-billed Gull	28	54	This study

In Table 9, the incubation periods of California and Ring-billed Gulls at Miquelon Lake are compared with those of gull species nesting along the marine coasts. Since incubation apparently takes slightly longer in larger gulls of the same genus, comparative measurements on adult weight are shown. There appears to be no adaptive shortening in the incubation periods of the inland-nesting California and Ring-billed Gulls when weight differences are considered.

Table 9. Incubation periods and adult weights in seven species of gulls.

Species	Mean incubation period ± SE in days	Sample	Authority	Mean adult weight (grams)	Sample	Authority
Herring Gull	27.2 ± 0.08	67	Paludan, 1951	1048	63	Barth, 1967
Glaucous-winged Gull	26.9 ± 0.08	128	Vermeer, 1963	1051	31	Vermeer, 1963
California Gull	26.6 ± 0.09	57	This study	769	39	This study
Lesser Black-backed Gull	26.1 ± 0.09	55	Paludan, 1951	736	19	Barth, 1967
Mew Gull	25.8 ± 0.25	50	Barth, 1955	386	26	Barth, 1967
Ring-billed Gull	25.0 ± 0.10	64	This study	497	39	This study
Black-headed Gull	22.8 ± 0.07	156	Ytreberg, 1956	297	18	Kruuk, 1964

4.5 First flight and colony departure. Table 10 presents the ages at first flight of California and Ring-billed Gulls studied in 1964.

Table 10. Distribution of ages at first flight in California and Ring-billed Gulls in 1964.

Species	Age in days at first flight											
	34	35	36	37	38	39	40	41	42	43	44	Mean age ± SE
California Gull	0	0	4	3	0	1	1	1	5	0	4	40.0 ± 0.72
Ring-billed Gull	1	2	6	12	4	2	2	1	0	0	0	37.2 ± 0.28

The average age at first flight for Ring-billed Gulls was 37.2 days, and for California Gulls, 40 days. This meant that the Ring-billed Gulls were calculated to fledge on the average by July 11 and the California Gulls by July 16 in 1964.

Judging from observations made on July 5, 9, 10 and 13 in 1965 at two gull colonies at the north end of Beaverhill Lake, it seemed that the chronology of the gull breeding cycles there were similar to those at Miquelon Lake. The first fledglings of both species at Beaverhill Lake were observed on July 9.

The chicks of two coastal breeding species of gulls, the Herring Gull (Paynter, 1949) and the Glaucous-winged Gull on Mandarte Island fledged on the average at 42 and 44 days respectively. Since these two species are larger (Table 9) than California and Ring-billed Gulls, it is expected that they would fledge slightly later.

From counts made every three days in July, 1964 of the number of fledglings present on island A, it was estimated that fledglings of both species remained on the island on the average for 11 days after fledging. The Glaucous-winged Gull fledglings remained on Mandarte Island for an average of 14 days after first flight which does not differ much from the post-fledging period spent by gulls in the Miquelon Lake colony.

Most families of California and Ring-billed Gulls appear to break up at the colony as the counts show that the parents slightly preceded

the fledglings in departure from island A (Table 11).

Table 11. Decline in numbers of California and Ring-billed Gulls on island A at Miquelon Lake from July 26 to August 4, 1964.

Date	California Gull Adults	 Fledglings	 Adult/Fledgling Ratio	Ring-billed Gull Adults	 Fledglings	 Adult/Fledgling Ratio
July 26	45	116	0.39	3	17	0.17
July 28	26	71	0.37	0	2	0.0
July 30	10	40	0.25	0	2	0.0
July 31	12	35	0.29	0	2	0.0
August 3	1	18	0.05	0	1	0.0
August 4	0	1	0.0	0	1	0.0

The presence of the chicks appears to be the chief reason for the adults to remain on the nesting grounds. In 1965, neither species produced fledglings. On July 2 of that year, only four adults of each species along with five California and three Ring-billed Gull chicks were present on island A. On July 3, the eight fledglings had disappeared and the adults had departed. Gulls also left island B by that date. The earlier departure of the parents than the fledglings in 1964 and the much earlier disappearance of the adults from the breeding grounds in 1965 than in the preceding year may indicate that the food supply in July was scarce at Miquelon Lake. Surveys conducted to investigate the fish supply of Miquelon Lake showed the scarcity of fish there (C. Hunt pers. comm.). During a visit to Lac la Biche (120 miles north-east of Miquelon Lake) in the last week of August, 1966, I observed that adults and fledglings of the California Gulls were common in the vicinity of their nesting

habitat. The gulls' residence for a long period after fledging at Lac la Biche may be related to a large fish supply in this lake. More than 1,000,000 lb. of fish are caught per year in Lac la Biche (C. W. Scott, pers. comm.).

I believe that in most cases once the fledglings leave the islands in Miquelon Lake on which they were hatched, they do not return, but disperse to areas where food is readily available. One of these areas is Edmonton, where garbage attracts large numbers of gulls. I observed several colour-banded juveniles of both species, banded at Miquelon Lake, during a visit to the Edmonton garbage dump in August of 1964. Although several visits were made to Miquelon Lake after the second week of August, no adults or juveniles of either species were observed on the islands.

5. REPRODUCTIVE SUCCESS

5.1 Clutch Size. The clutch sizes of California and Ring-billed Gulls for the years 1964 and 1965 are compared in Table 12.

Table 12. Clutch size of California and Ring-billed Gulls in 1964 and 1965 at Miquelon Lake.

Clutch size	No. of clutches			
	California Gull		Ring-billed Gull	
	1964	1965	1964	1965
1	2	1		2
2	35	33	30	76
3	168	97	227	345
4	1		8	11
5				1
Total	206	131	265	435
Mean clutch size ± SE	2.82 ±0.03	2.73 ±0.04	2.92 ±0.02	2.85 ±0.02

The average clutch size of each of the gull species in 1965 was smaller than that of the previous year. This may have resulted from inaccuracy of data in 1965, since more human and predatory disturbances occurred that year, which may have led to greater egg loss form the nests between my visits. Table 12 shows also an interspecific difference in the mean clutch size in both 1964 and 1965. The significant difference in the mean clutch sizes may be related to the denser concentration of nests of the Ring-billed Gulls. Increased nest density may facilitate accidental laying by two females in one nest. The clutch with five eggs, listed in Table 12, may have been produced in this manner. Three eggs were found in the nest on one day and five the following. Since the usual time interval between the laying of successively laid eggs in

a clutch was two days, it is not likely that one female produced two eggs within one day.

Studies elsewhere also show that clutches with more than three eggs occur more frequently in Ring-billed Gulls than in California Gulls. Behle and Goates (1957) reported that one California Gull nest out of four hundred observed had more than three eggs. Johnston and Foster (1954) found that of 693 Ring-billed Gull clutches, many of which were within three feet of each other, 20, 17 and 8 clutches contained 4, 5 and 6 eggs respectively. This may also point to accidental laying by two females in one nest.

In Table 13, the average clutch sizes in California and Ring-billed Gulls are compared with those of four other species of the genus Larus which breed along the coast. Only studies in which more than 200 clutches were observed are included in Table 13.

Table 13. Comparison of the mean clutch size in six species of gulls

Species	No. of clutches studied	Mean clutch size	Location	Authority
California Gull	337	2.77	Canada	This study
Ring-billed Gull	700	2.87	Canada	This study
"	693	2.84	U.S.A.	Johnston & Foster 1954
Glaucous-winged Gull	758	2.77	Canada	Drent et al., 1964
Herring Gull	1011	2.38	Canada	Paynter, 1949
"	220	2.76	England	Harris, 1964
"	217	2.91	Denmark	Paludan, 1951
Lesser Black-backed Gull	242	2.75	Denmark	Paludan, 1951
Black-headed Gull	421	2.90	Norway	Ytreberg, 1956

It can be seen that the mean clutch sizes of the California and Ring-billed Gulls are similar to those of the coastal breeding gulls.

5.2 Loss of eggs. Table 14 presents the egg losses in California and Ring-billed Gulls in 1964 and 1965. At my first arrival on island A in the spring of 1964, work still had to be done on the observation tower and this, with my frequent movements in the immediate vicinity of the tower, caused a disturbance resulting in desertion of 264 (56%) of 470 nests of the California Gulls and 50 (16%) of 315 nests of the Ring-billed Gulls. The egg losses from the deserted nests are omitted from Table 14.

Table 14. Loss of eggs in two gull species at Miquelon Lake.

Year	Species	Island	No. of nests	No. of eggs laid	Loss of eggs	
					No.	%
1964	California Gull	A	206	580	150	25.8
1964	Ring-billed Gull	A	265	772	107	13.8
1965	California Gull	A	87	233	53	22.7
1965	California Gull	B	44	125	40	32.0
1965	Ring-billed Gull	A	58	148	86	58.1
1965	Ring-billed Gull	B	378	1093	955	87.4

The percentage of eggs lost by California Gulls was similar in 1964 and 1965. However, the loss suffered by Ring-billed Gulls increased significantly in 1965. The egg losses suffered by California Gulls in 1965 did not differ significantly between the islands. Ring-billed Gull losses were significantly higher on island B in that year.

Table 15 presents the fate of the eggs of both species which failed to hatch.

Table 15. Analysis of failure of eggs to hatch in two gull species in 1964 and 1965. The percentage of total number of eggs laid appears in brackets.

Cause	California Gull No. of eggs		Ring-billed Gull No. of eggs	
	1964	1965	1964	1965
Infertility or embryonic death	76 (13.1%)	26 (7.3%)	62 (8.0%)	554 (44.7%)
Disappeared and presumed eaten	61 (10.5%)	60 (16.8%)	39 (5.0%)	465 (37.5%)
Died in pipping	6 (1.0%)	4 (1.1%)	6 (0.8%)	5 (0.4%)
Incubation ceased*	7 (1.2%)	3 (0.8%)		17 (1.4%)
Total egg loss	150 (25.8%)	93 (26.0%)	107 (13.8%)	1041 (84.0%)

* Eggs lost as a result of parents dying or eggs buried in the nest.

The egg losses for the California Gulls in both years and the Ring-billed Gulls in 1964 were similar to those for other gulls studied (Harris, 1964; Drent et al. 1964). Table 15 shows that both the losses of the categories "infertility or embryonic death" and "disappeared and presumed eaten" increased significantly for the Ring-billed Gulls in 1965. Many of the eggs which did not hatch were cracked and these were frequently observed to be eaten by the parents. Tinbergen et al. (1962) observed also that Black-headed Gulls, which usually do not attack an undamaged egg, devoured an egg once it had been broken. Since the Ring-billed Gulls were observed to eat many of their own decayed and cracked eggs, most of the egg loss of this species in 1965 may have been the result of a higher rate of hatching failure. When the Ring-billed Gull eggs did not hatch at the expected time in 1965, 420 eggs on island B were opened and examined. There were no embryos in 97% of them, which indicated either infertility or early embryonic death.

Recent work on the adverse effects of insecticide contamination led me to submit six decayed eggs of Ring-billed Gulls from island A on June 30, 1965, for an analysis of chlorinated hydrocarbons. The analysis, based on the wet weight of the composite sample, disclosed the presence of 0.038 ppm DDT, 2.0 DDE, 0.029 DDD, and 0.028 dieldrin*.

*Chemical names of DDT, DDE and DDD and dieldrin are 2,2 Bis (p-chlorophenyl)-1,1,1-trichloroethene; 2,2 Bis (p-chlorophenyl-1, 1-dichloroethylene; 2,2 Bis (p-chlorophenyl)-1,1-dichloroethane and 1,2,3,4,10,10-hexachloro-6,7 epoxy-1,4,4a,5,6,7,8,8a-octahydro-1,4-endo-exo-5,8 dimethanohaphthalene, respectively.

On July 13, 1965, two Ring-billed Gull eggs from Beaverhill Lake, which were at the point of hatching, were submitted for an analysis of chlorinated hydrocarbons. A comparable analysis disclosed the presence of 5.18 ppm DDE and a trace of DDT which is at least twice the total level of chlorinated hydrocarbons present of that in the decayed eggs of Ring-billed Gulls at Miquelon Lake. Lockie and Ratcliffe's (1964) study on insecticide residues in the eggs of Golden Eagles (Aquila chrysaetos) in Scotland showed that there is no evidence that concentrations of dieldrin below one ppm affected the reproductive success of this species adversely. Therefore it seems unlikely that the presence of 0.028 ppm dieldrin in the analyzed eggs from Miquelon Lake was responsible for infertility or embryonic death. Keith (1966) found that in 115 nests of Herring Gulls at Lake Michigan 30 - 35% of the eggs did not hatch. Nine eggs from this colony were analyzed for chlorinated hydrocarbon residues with the following results (based on wet weight): averages of 19 ± 3 ppm of DDT, 202 ± 34 of DDE, and 6.0 ± 0.9 of DDD. The egg loss in the Ring-billed Gull eggs (84%) at Miquelon Lake in 1965 appeared to be considerably greater than in the Herring Gulls in Keith's study. The pesticide contamination observed in the Ring-billed Gull eggs cannot be held responsible for hatching failure.

Data on levels of chlorinated hydrocarbons in the adult gulls were sought as contamination levels in the adults may have led to aberrations in incubation behaviour and subsequent parental neglect. Eight Ring-billed and eight California Gulls taken in June, 1965 at Miquelon Lake, and eight Ring-billed Gulls taken in July, 1965 from a Beaverhill Lake colony were analyzed for the presence of residues of chlorinated hydrocarbons. The Ring-billed Gulls from Beaverhill

Lake were analyzed, because I estimated the fledging success there in 1965 to be the same or better than of this species at Miquelon Lake in 1964. The brains and uropygial glands were selected for analysis because these tissues are known to accumulate high concentrations of insecticides (V. Lewin, pers. comm.). The results of the analyses, shown in Table 16, are difficult to interpret, but in both brain and uropygial tissue the order of DDE contamination was: Ring-billed Gulls, Miquelon Lake; California Gulls, Miquelon Lake; Ring-billed Gulls, Beaverhill Lake. The results obtained on hydrocarbon levels in adult gulls may not be representative, since one highly contaminated gull may bias the mean contamination level in a composite sample.

Table 16. Analyses of composite samples of brains and uropygial glands of gulls for chlorinated hydrocarbons.

Tissue	Location	Date	No. in composite sample	Mean residue content in ppm. of wet weights California Gull	Ring-billed Gull
Brain	Miquelon Lake	Mid-June	8	2.6 DDE 0.25 DDD 0.07 DDT	23.0 DDE 0.12 DDD 0.06 DDT
Brain	Beaverhill Lake	Mid-July	8		0.37 DDE 0.03 DDD 0.01 DDT
Uropygial gland	Miquelon Lake	Mid-June	8	20.0 DDE 0.38 DDD 0.16 DDT	30.0 DDE 0.40 DDD 0.14 DDT
Uropygial gland	Beaverhill Lake	Mid-July	8		12.7 DDE 0.36 DDD 0.23 DDT

In 1965, Ring-billed Gulls subsisted mainly on waste grain left in the field throughout April and the first half of May (section 7). The diet of the California Gull at this time was more heterogeneous. Since the high level of insecticide residues in the Ring-billed Gulls at Miquelon Lake seemed to be a local phenomenon, a composite sample of 32 pellets composed of oats and barley from Ring-billed Gulls at Miquelon Lake was analyzed. The analysis showed the presence of 3.0 ppm DDE, 0.5 DDT, 0.01 DDD and a trace of dieldrin. The insecticide residue content in the pellets may have come from the digestive juices of the gulls and/or small remains of insects possibly interspersed among the grain. If the insecticide residues originated in the grain and formed the chief source of the high level of insecticide residues in the Ring-billed Gulls at Miquelon Lake, the contaminated grain must have been locally distributed, otherwise the Ring-billed Gulls at Beaverhill Lake would have shown quantities of chlorinated hydrocarbons similar to the ones at Miquelon Lake.

The greatest mortality occurred in eggs which were laid on island B (Table 14) and thus early in the season. The ice conditions prevented human visitation of island B prior to May 7, at which time the egg-laying process was advanced. Ring-billed Gull egg mortality was lower on island A than on island B even though I occupied a cabin on the former. Thus I believe that human disturbance may be disregarded as a cause of either low fertility or early death of the embryos.

In Table 17, the percentage of clutches started by Ring-billed Gulls on island A and B has been calculated for different periods of the laying season in relation to a snowstorm which lasted the night on May 17, 1965. The temperature dropped to 32°F that night. The California Gulls nesting close to the cabin on island A were observed to continue incubating

throughout the storm. The Ring-billed Gulls could not be observed at this time.

Table 17. Comparison of progress in clutch commencement between Ring-billed Gulls nesting on islands A and B in relation to a snowstorm occurrence on May 17, 1965.

Time period	Percentage of clutches started in the Ring-billed Gull	
	island A	island B
May 3 - 9	2.2	66.0
May 10 - 16	88.9	28.1
May 17	—	0.7
After May 17	8.9	5.2

MacMullan and Eberhardt (1953) found that pheasant embryos are progressively more vulnerable to chilling as incubation progressed. Moreng and Bryant (1956) reported that chick embryos exposed to low temperatures after the fourth day of incubation showed a drastic reduction in hatchability. It can be seen in Table 17 that laying in the Ring-billed Gulls was more advanced by May 17 on island B than on island A. If the Ring-billed Gull eggs were exposed to the snowstorm, the more advanced embroys of this species on island B would be more susceptible to chilling than those less advanced on island A. It will be recalled that the loss of Ring-billed Gull eggs was significantly greater on island B than on island A.

The effect of the snowstorm cannot be held solely responsible for the extensive egg mortality in the Ring-billed Gulls, otherwise the hatching success of the California Gulls would probably have been similarly

affected. The Ring-billed Gulls were observed to be much more excitable than the California Gulls. Extensive nocturnal predation occurred during the 1965 breeding season as will be discussed later. If nocturnal predation occurred during the storm on May 17, the Ring-billed Gulls would probably be more easily disturbed and leave their eggs exposed to chill longer than the California Gulls. Emlen et al. (1966) observed that Ring-billed Gull eggs in Michigan became chilled as a result of panic flights of the gulls which were initiated by a visiting nocturnal raccoon. They (1966: 679) report: "The effects of these mass exoduses were apparent. The eggs and newly hatched young were cold; the cheeping heard shortly after a mass departure soon subsided as the chicks became chilled in the 5° to 15°C temperatures. A sampling of 87 eggs on June 5 revealed that 32 per cent of the embryos were dead. Daytime checks of nests on the days following the upflights showed a nightly mortality of between 30 and 80 per cent of one-to two-day-old chicks, and a check of the site in late June indicated that very few, if any, young had been produced." Although the cause of the extensive egg mortality of the Ring-billed Gulls at Miquelon Lake in 1965 is unknown, a combination of nocturnal predation and bad weather may explain the hatching failure of this species in that year.

Table 18 shows the number of California and Ring-billed Gull eggs which disappeared or were eaten during laying and the time of incubation. Only the 1964 data are used since conditions were more natural during laying and incubation in that year than in 1965. The time when Glaucous-winged Gull eggs disappeared or were eaten on Mandarte Island in 1962 are shown for comparison.

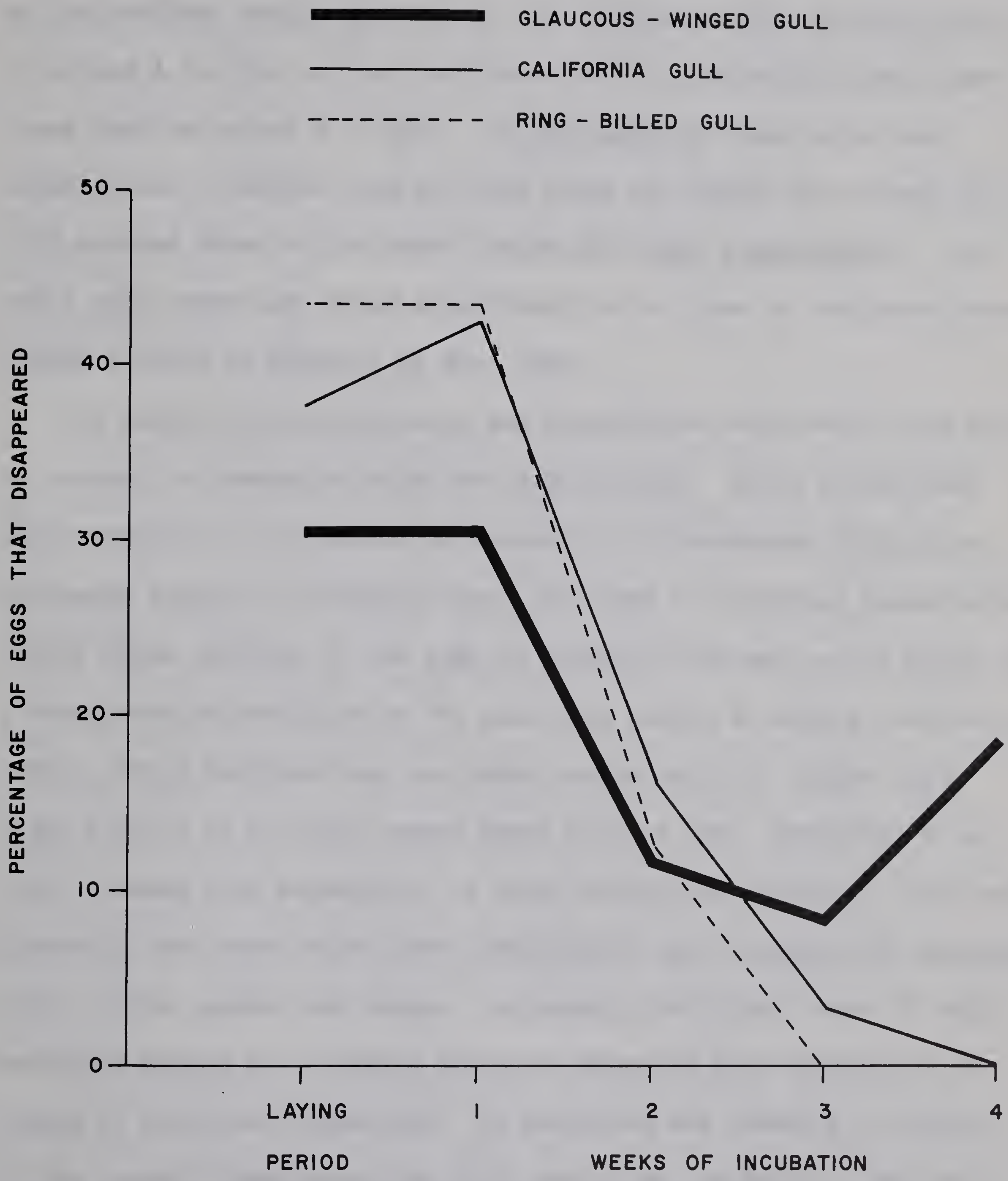
Table 18. Number of eggs disappeared or eaten versus time during laying and incubation in three gull species. In brackets, the percentage of total number of eggs laid.

Time of laying and incubation period	No. of eggs disappeared or eaten Ring-billed Gull	California Gull	Glaucous-winged Gull
Laying*	17 (2.2%)	23 (4.0%)	18 (1.3%)
week 1	17 (2.2%)	26 (4.5%)	18 (1.3%)
week 2	5 (0.6%)	10 (1.7%)	7 (0.5%)
week 3	0	2 (0.3%)	5 (0.4%)
week 4	0	0	11 (0.8%)
Total no. of eggs disappeared or eaten	39 (5.0%)	61 (10.5%)	59 (4.3%)

*Laying averaged 4 days for California and Ring-billed Gulls and 4½ days for the Glaucous-winged Gulls.

The majority of eggs disappeared or were eaten, presumably by gulls, during laying and in the first week of incubation in all three gull species. Ytreberg (1956) reported that Black-headed Gulls lost four times as many eggs per time unit in the laying period than during incubation. The reason that most of the eggs disappeared at the time reflects the gulls greater tendency to leave the nests when there is a disturbance. It appears that one of the roles of incubation, besides providing the warmth necessary for the development of the embryo, is to reduce egg predation. In Fig. 8, the number of eggs disappeared or eaten during laying and in the subsequent weeks of incubation are compared on a relative basis, that is the total number of eggs disappeared or eaten in each species is taken as 100%. It can be seen that the rates of egg disappearance were similar for California and Ring-billed Gulls. The rate of disappearance in the Glaucous-winged Gulls differed chiefly in the last week of incubation, but the overall rate of disappearance seems similar to that of the inland-nesting species.

Fig. 8. Percentage of eggs disappearing during laying and subsequent weeks of incubation in three gull species.


GLAUCOUS - WINGED GULL
CALIFORNIA GULL
RING - BILLED GULL
PERCENTAGE OF EGGS THAT DISAPPEARED
50
40
30
20
10
0
LAYING
PERIOD
1
2
3
4
WEEKS OF INCUBATION

Three eggs of the California Gulls in 1964 and 3 and 17 eggs of the California and Ring-billed Gulls respectively were lost in 1965 as a result of parents being killed by a predator. Of the adults killed by the predator during incubation, one California Gull was found dead on island A in 1964 and one California and six Ring-billed Gulls were found dead on island B in 1965. In all cases the dead birds were decapitated. Feathers from the area where the bodies were found in 1965 matched those of the Great Horned Owl (Bubo virginianus). Ten adult gulls were also found decapitated on or close to the nests, when I made a visit to island A in May, 1963.

No adults of the California and Ring-billed Gulls were found dead as a result of predation after the eggs hatched. Kruuk (1964) found that predation on the adults in a colony of Black-headed Gulls also decreased sharply at hatching time. The lack of nocturnal predation on adults after hatching of the eggs at Miquelon Lake may be the result of a changeover of predation by the owls from adults to chicks (section 5.3). Austin (1946) reported that one Great Horned Owl in a single night might kill 15 to 20 adult Common Terns at Cape Cod. Errington et al. (1940) showed from examination of Great Horned Owl pellets in Iowa and Wisconsin that these birds prey considerably upon breeding and migrating coots, rails, grebes and ducks. In summary, the chief cause of adult mortality during the breeding season at Miquelon Lake appeared to be caused by the Great Horned Owl. No predation was observed on adults of the coastal Glaucous-winged Gulls during my residence on Mandarte Island in the summers of 1961 and 1962.

5.3 Loss of chicks. Table 19 summarizes the fledging success of the California and Ring-billed Gulls on island A in 1964. No chicks fledged in 1965.

Table 19. Fledging success of two gull species at Miquelon Lake in 1964

Species	Total	Young Fledged Per nest	Young Fledged Percentage of eggs	Young Fledged Percentage of chicks
California Gull	210	1.0	36.2	48.8
Ring-billed Gull	265	1.0	34.3	39.9

In July, 1965, I investigated two gull colonies at the north end of Beaverhill Lake. On an island of approximately one acre, there was a colony of about 200 pairs of California Gulls. I estimated that 1.4 chicks fledged per pair of California Gulls on this island. A few miles away about 3000 pairs of Ring-billed Gulls and less tha~~t~~n 50 pairs of California Gulls nested on an island of approximately 25 acres. No count could be made of the Ring-billed Gull chicks on the large island, but I estimated success to be the same as or better than that of this species at Miquelon Lake in 1964. Hence, the absence of fledglings at Miquelon Lake in 1965 appeared to be a very local phenomenon.

Table 20 shows the loss of chicks in both species on island A in 1964 and 1965. The loss of eggs in 17 nests of the California Gulls on island A in 1965 was included in Table 14, but the loss of chicks from these nests is omitted from Table 20 since they were used for an exchange experiment with chicks on island B.

Table 20. Causes of mortality among gull chicks on island A in 1964 and 1965.

Causes	California Gull		Ring-billed Gull	
	1964	1965	1964	1965
Disappeared	126 (57.3%)	85 (63.0%)	234 (58.5%)	39 (62.9%)
Predation				
Pecked to death by gulls	31 (19.5%)	3 (20.7%)	34 (17.5%)	3 (16.1%)
Eaten by gulls	11	4	31	2
Eaten by Great Horned Owl (?)*	0	19	3	5
Eaten by Red-tailed Hawk	1	0	2	0
Eaten by weasel (?)	0	2	0	0
Other				
Carcasses found, cause unknown	37 (16.8%)	15 (11.1%)	84 (21.0%)	11 (17.8%)
Exposure during rain	7 (6.4%)	6 (5.2%)	0 (3.0%)	2 (3.2%)
Disease	2	1	6	0
Crippling	1	0	3	0
Blindness	1	0	0	0
Suffocation on food	3	0	1	0
Crushed by observer	0	0	2	0
Total deaths	220 (100%)	135 (100%)	400 (100%)	62 (100%)

*Included is gull chick mortality caused through predator-induced exposure.

The cause of death in the majority of cases could not be ascertained because the chicks had disappeared between my visits.

In the category "pecked to death by gulls" are included gull chicks which were pecked to death by adults when wandering away from their parents. The habit of adults attacking strange chicks was the primary cause of chick mortality in Glaucous-winged Gulls on Mandarte Island. Most of the chick mortality observed in Ring-billed Gulls in Michigan, U.S.A. (Emlen, 1956), in a Herring Gull colony in Denmark (Paludan, 1951) and in a Herring Gull colony in New Brunswick, Canada (Paynter, 1949) also resulted from this agressive behaviour of the adults.

Colour-bands of chicks which were eaten were recovered in pellets and on chick legs which were left after the body had been devoured. California and Ring-billed Gulls were observed preying upon chicks, mostly less than one week of age, of their own species as well as those of the other species. The California Gulls preyed upon chicks much more than the Ring-billed Gulls.

Chicks were found decapitated on island A in 1964 and in 1965. Feathers from the area where the bodies were found matched those of the Great Horned Owls. The calls of this predator were heard on several evenings near island A, Miquelon Lake. I observed a Great Horned Owl in a Ring-billed Gull colony at Beaverhill Lake in July, 1965. The owl was roosting during the day in willow bushes beside this colony. Two decapitated gull chicks were found nearby.

Twelve three and four-week-old chicks were also found decapitated on island B in 1965. The predator was again considered to be the owl as evidenced by its feathers at the site of the kills. Chicks which had just hatched and others a few days of age were found chilled and dead at the same time that the decapitated chicks were found. At least

10 chicks died in this way, but there may have been many more. Hence, parents appeared to neglect their chicks on nights when the nocturnal predator appeared.

A Red-tailed Hawk (Buteo jamaicensis) was seen to kill a three-week-old California Gull chick on island A in 1964. I located the nest of this hawk, which contained two newly hatched young. Colour-bands from two Ring-billed Gull chicks were found in pellets below the nest. Two other nests occupied by Red-tailed Hawks were found near Miquelon Lake. They were both farther from the gull colony. No gull chick remains were found either in or below these nests. No gull chick remains were found in pellets of the Red-tailed Hawk or observed being killed by this predator in 1965.

Two one-day-old California Gull chicks on island A were found blood-stained and showed puncture wounds on the neck and head. They subsequently died. They may have been victims of a least weasel (Mustela rixosa). Least weasels were seen several times on island A. On one occasion, I observed two of them on the island. It is probable that they were preying on Microtus pennsylvanicus, which were very numerous on the island. Least weasels may have been responsible for the disappearance of some of the newly-hatched chicks, but they are not thought to be important predators on young gull chicks because, if adult gulls observed them around the nest, the weasels would run the risk of being attacked. The remains of one least weasel were recovered from a gull pellet, indicating that predator may become prey.

Gull chicks died as the result of rainstorms. Seven California Gull chicks died in 1964 as the result of human disturbance prior to a rainstorm. The distrubance caused chicks to hide away from the

nest where they were not brooded by the adults and thus became completely wet and chilled. In this condition, they appeared unable to return to the nest-site and died from exposure. Other chicks which had been exposed to the same storm on the shore were brooded by the parents on the beach and survived. Very young gull chicks appear to be vulnerable to persistent rain under natural conditions. The death of six California and two Ring-billed Gull chicks within their first three days of life apparently resulted directly from rainfall which persisted over three successive days in the last week of June, 1965.

Two California Gull chicks died while eating ground squirrels. Each of them was found with the hind limbs of a ground squirrel protruding from the mouth. Death appeared to have resulted from suffocation. One California and one Ring-billed Gull chick died as a result of the ingestion of a large piece of bone.

The chick mortality in the different categories in Table 20 can be compared between species and seasons. The percentage of chicks which was missing did not vary significantly between the species. The slight increase of the number of chicks which disappeared in 1965 over 1964 may result from nests being checked less frequently during the early chick stage in 1965 (once every three days) than in 1964 (once each day).

A higher proportion of gull chicks were found pecked to death by gulls in 1964 than in 1965. The greater chick mortality from this cause in 1964 may have resulted from the greater nesting densities in that year which may have enhanced more agressive encounters. The smaller proportion of remains and colour-bands of chicks eaten by gulls found in 1965 probably is an artifact, the chick remains being more difficult to find in the latter season because of the lush vegetation.

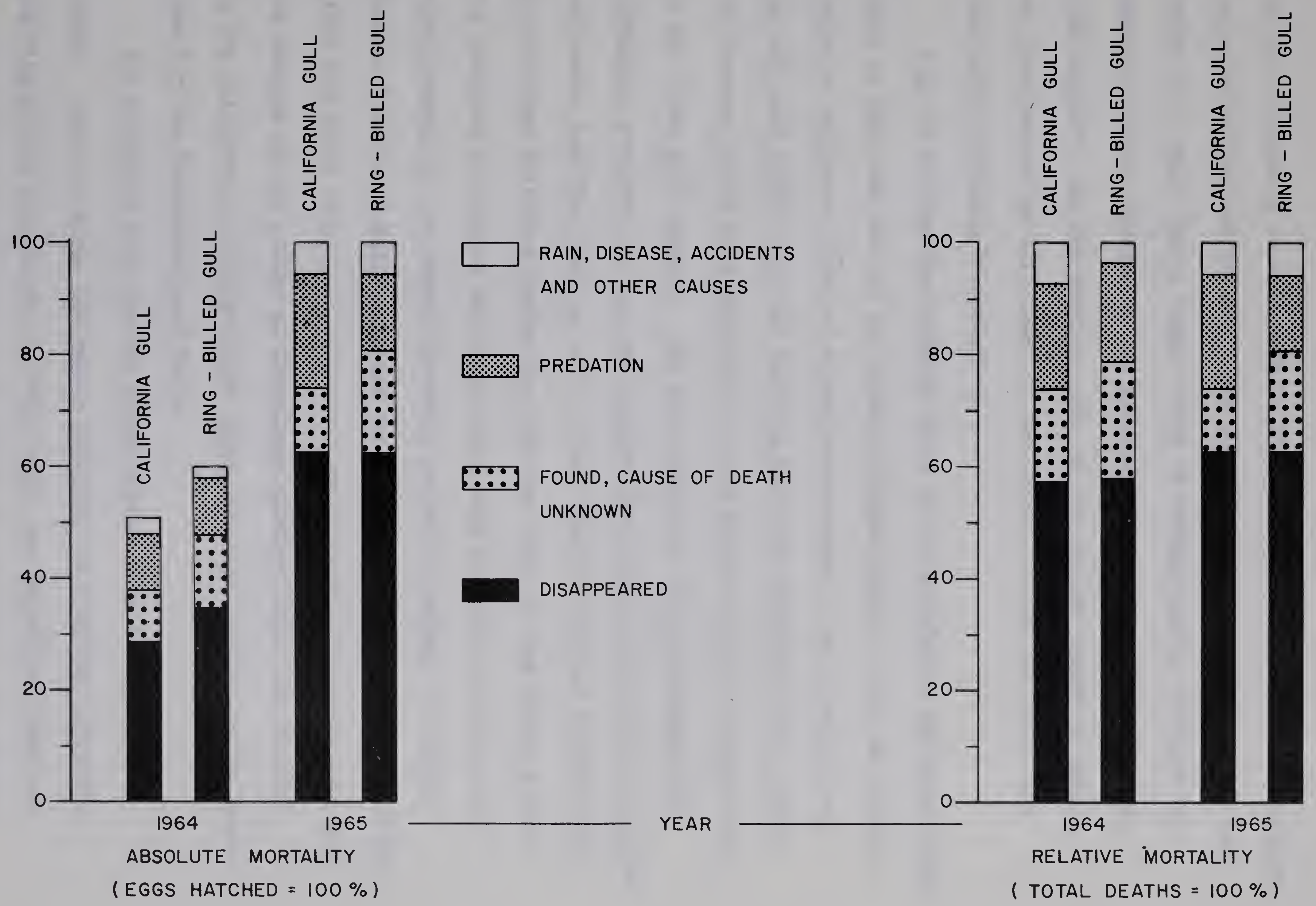
Many more gull chicks, presumably victims of the Great Horned Owl, were found decapitated in 1965 than in 1964. Although predation by this predator varied seasonally, the total percentage of chicks preyed upon did not vary significantly between the species or the years.

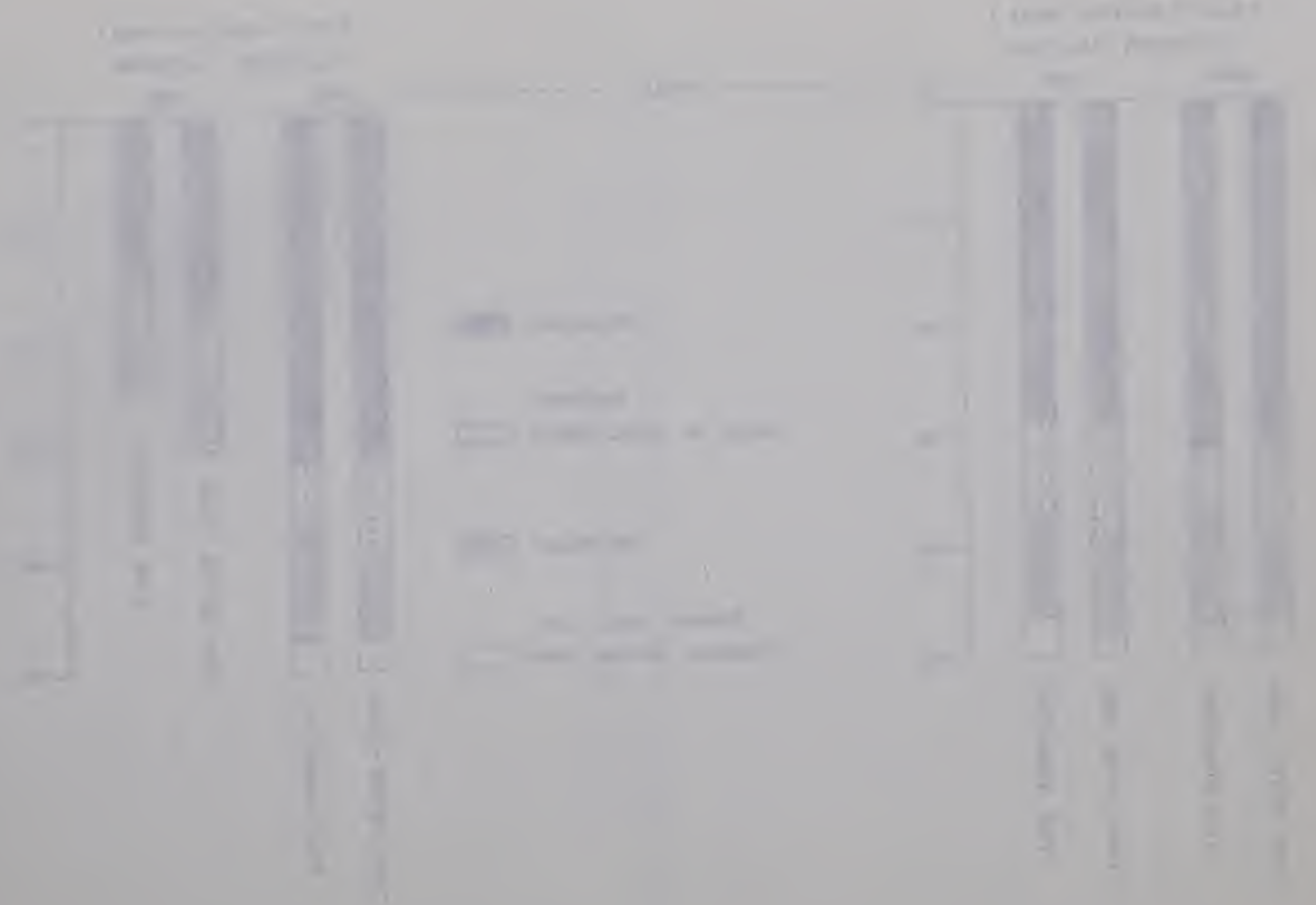
The total proportion of carcasses of which the cause of death was unknown, found in 1964 was significantly greater than in 1965. This may have been the result of no chicks reaching their fifth week of life (at which state carcasses can readily be found) in 1965.

The mortality factors in chicks of California and Ring-billed Gulls on island A between 1964 and 1965 are compared on an absolute and relative basis in Fig. 9. It is evident that deaths from all measured factors increased in the 1965 season, so that no single factor can be considered the cause of the poor reproductive success in that year. Parental neglect describes the state of affairs without explaining it. Perhaps the increased visitation by the Great Horned Owl helped to bring about a panicky state in the colony as did a raccoon in a colony of Ring-billed Gulls studied by Emlen et al. (1966).

In several studies on colonial species it has been shown that small groups had very little success. Patterson (1965) showed that those Black-headed Gulls breeding outside the main groups had very little success. Kruuk (1964) has demonstrated that the greater safety of eggs and young in larger groups in Black-headed Gulls is related to more efficient anti-predator behaviour in the larger groups. In 1966, Dwernychuk resided on island A at Miquelon Lake and found (pers. comm.) only 12 nests of California Gulls there. Approximately 10 young fledged from these nests. No Great Horned Owl predation was observed at Miquelon Lake that year. Hence the smaller group of gulls

Fig.9 Comparison of absolute and relative mortality of California and Ring-billed Gull chicks on island A in 1964 and 1965.


CALIFORNIA GULL
RING - BILLED GULL
CALIFORNIA GULL
RING - BILLED GULL
100
80
60
40
20
0
1964
1965
ABSOLUTE MORTALITY
(EGGS HATCHED = 100 %)
RAIN, DISEASE, ACCIDENTS AND OTHER CAUSES
PREDATION
FOUND, CAUSE OF DEATH UNKNOWN
DISAPPEARED
YEAR
CALIFORNIA GULL
RING - BILLED GULL
CALIFORNIA GULL
RING - BILLED GULL
100
80
60
40
20
0
1964
1965
RELATIVE MORTALITY
(TOTAL DEATHS = 100 %)



per se on island A in 1965 than in 1964 was not the cause of the complete reproductive failure in 1965. But nocturnal predation may be much more severe on a small than a large colony of nesting gulls. Besides the predator-induced absence of the parents, causing young chicks to die from exposure, the few warning calls of the smaller number of adults may also reduce the efficiency of the chicks to hide and hence make them more vulnerable to predation.

Fig. 10 relates the fledging rates in the California and Ring-billed Gulls in 1964 and that of the Glaucous-winged Gulls in 1962 on Mandarte Island to different times of clutch commencement. The fledging rate per egg laid rather than the fledging rate per clutch is shown, since the average clutch size declined with the progress of the laying season in all three gull species. The mean number of Glaucous-winged Gull fledglings produced per egg was similar for clutches started in the first six weeks, but the fledging rate of this species declined significantly for clutches initiated during the last two weeks of the laying period. The combined California and Ring-billed Gull fledging rate decreased significantly in the second bi-weekly period of laying. No chicks fledged from three California and two Ring-billed Gull clutches started after the first four weeks of clutch commencement. It can be seen that the decline of the number of fledglings produced from late clutches in the California and Ring-billed Gulls came much earlier in the season than for the Glaucous-winged Gulls.

The mortality rate for the chicks varies with the age of the chicks. Table 21 shows the weekly mortality rate of the California and Ring-billed Gull chicks in 1964, which was calculated from the number observed being alive at the onset of each week. The weekly mortality rates for 1965 have been omitted from Table 21, since it

Fig. 10. Fledging rates of three gull species for clutches started during consecutive bi-weekly periods. Numbers on top of bars indicate number of clutches started during each bi-weekly period and those in brackets, the mean clutch size for each bi-weekly period.

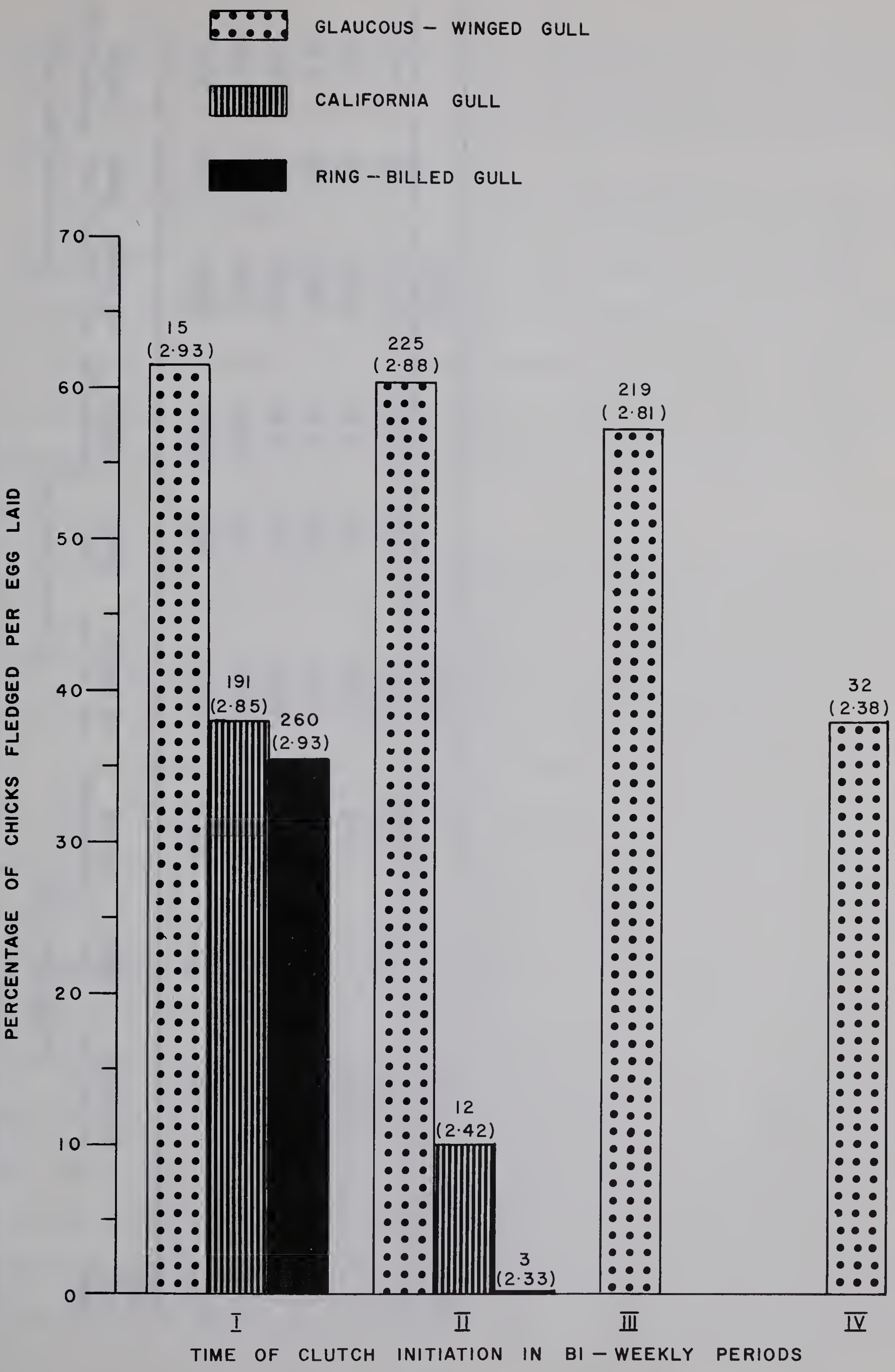

GLAUCOUS — WINGED GULL
CALIFORNIA GULL
RING — BILLED GULL
PERCENTAGE OF CHICKS FLEDGED PER EGG LAID
70
60
50
40
30
20
10
0
15
(2·93)
191
(2·85)
260
(2·93)
225
(2·88)
12
(2·42)
3
(2·33)
219
(2·81)
32
(2·38)
I
II
III
IV
TIME OF CLUTCH INITIATION IN BI — WEEKLY PERIODS

Table 21. Weekly mortality rates of the chicks in three gull species.

Week of Life	California Gull			Ring-billed Gull			Glaucous-winged Gull		
	No. alive at onset	No. dead	Percentage dying	No. alive at onset	No. dead	Percentage dying	No. alive at onset	No. dead	Percentage dying
1	430	135	31.4	665	220	33.1	1156	194	16.8
2	295	45	15.3	445	75	16.9	962	65	6.8
3	250	21	8.4	370	34	9.2	897	38	4.2
4	229	7	3.1	336	31	9.2	859	30	3.5
5	222	5	2.3	305	23	7.5	829	15	1.8
>5	217	7	3.2	282	17	6.0	814	12	1.5
No. fledged	210			265			802		

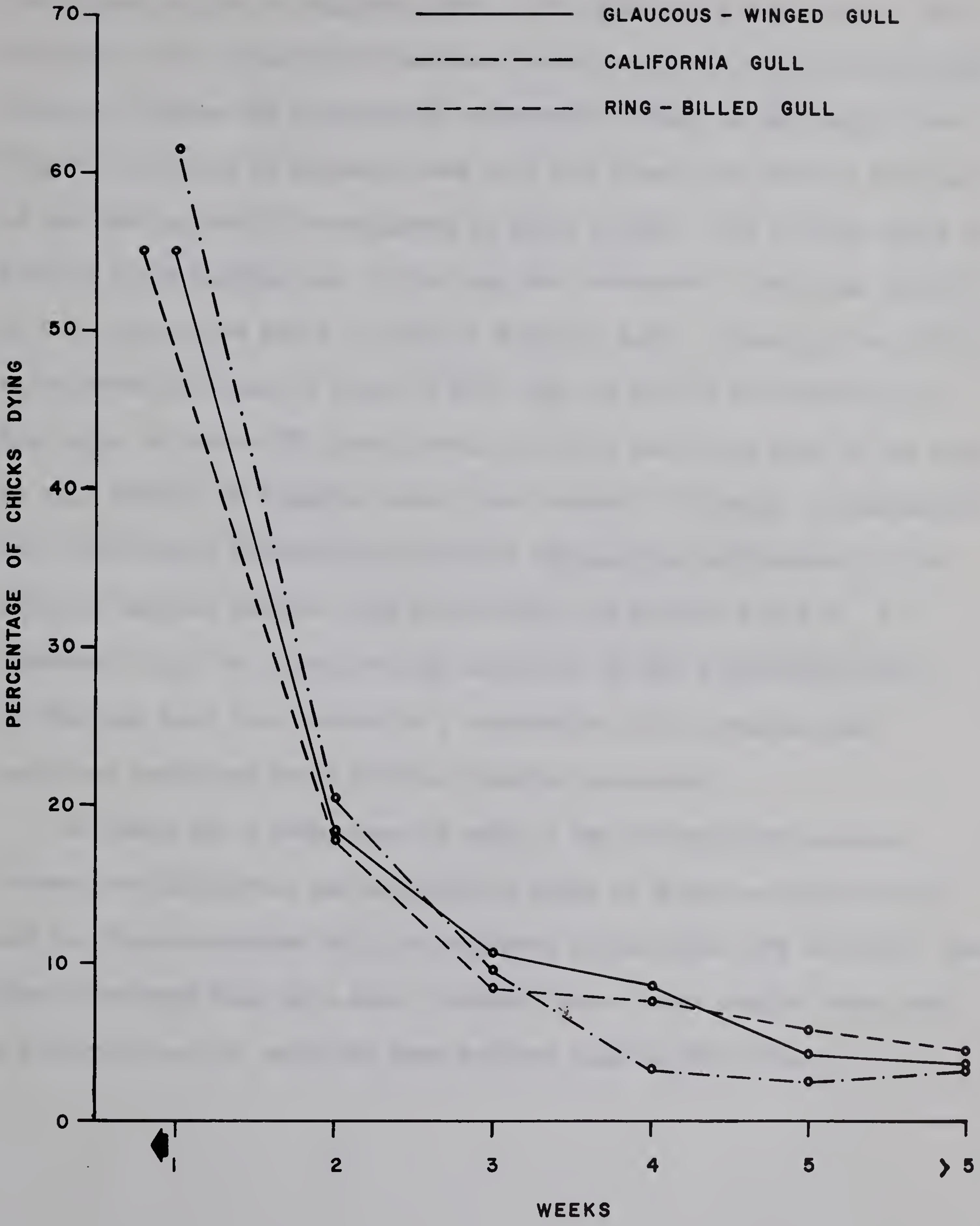
was an abnormal year for chick production at Miquelon Lake. The weekly mortality rates for the chicks of the Glaucous-winged Gulls on Mandarte Island in 1962 are shown for comparison.

The advanced state of vegetation in the first half of June in 1964 made it difficult to acquire data on the exact number of chicks which were still alive at the end of the first and second week of life. Therefore, the figures at the onset of the second and third week may be slightly biased as more chicks may have been alive at that time. It is apparent from Table 21 that the greatest chick mortality in all three species occurred in the first week of life.

In Fig. 11, the relative weekly mortality rates of the chicks are compared on the basis of total chick mortality per season in each species equalling 100%. It can be seen that the rates of weekly mortality were similar in the California, Ring-billed and Glaucous-winged Gulls.

Emlen (1956) in Michigan and Harris (1964) in Wales, on the basis of samples of 37 dead Ring-billed Gull chicks and 80 dead Herring Gull chicks, come to the conclusion that there was no evidence for a greater mortality in the first week of life of these species. On the other hand, Paludan (1951) and Fordham (1964) found that most of the gull chick mortality occurred in the first week of life. The samples of Emlen and Harris are biased as the loss of chicks through disappearance is not taken into account in their studies and as small chicks are more difficult to find than older and larger ones. On several occasions at Miquelon Lake, I observed that small chicks were swallowed whole by adult California Gulls. Furthermore, gull pellets at Miquelon Lake contained many numbered colour bands of chicks which had disappeared in their first week of life.

Fig. 11. Relative weekly chick mortality in three gull species


GLAUCOUS - WINGED GULL
CALIFORNIA GULL
RING - BILLED GULL
PERCENTAGE OF CHICKS DYING
70
60
50
40
30
20
10
0
1
2
3
4
5
> 5
WEEKS

5.4 Overall reproductive success. The complete failure to produce fledglings in 1965 at Miquelon Lake is not completely understood. The hypothesis that insecticide residues caused embryonic death is unproven; firstly, because the chlorinated hydrocarbon levels in the eggs of the Ring-billed Gulls at Miquelon Lake were 108 times less than in the eggs of the Herring Gulls investigated by Keith (1966). The Herring Gulls in Keith's study hatched 41% of the eggs laid compared to only 16% of that of the Ring-billed Gulls in 1965 at Miquelon Lake. Secondly, the total chlorinated hydrocarbon level of DDT, DDE and DDD in the Ring-billed Gull eggs at Beaverhill Lake (normal success) was twice that of the eggs of this species at Miquelon Lake (poor success). Thirdly, contamination with chlorinated hydrocarbons does not explain the differences in the hatching success between Ring-billed Gulls on islands A and B. A hypothesis that the extensive egg mortality in the Ring-billed Gulls in 1965 may have been caused by a combination of bad weather and nocturnal predation would fit the observed phenomena.

In Table 22, a comparison is made of the reproductive success between the California and Ring-billed Gulls at Miquelon Lake in 1964 and the Glaucous-winged Gulls on Mandarte Island from 1958 to 1962. The Glaucous-winged Gull data were obtained from a large sample taken over a five-year period, with the same methods used in this study.

Table 22. Reproductive success of three gull species

Species	Study period	Production per season per 100 nests Eggs	Hatched	Fledged	Authority
California Gull	1964	282	209	102	This study
Ring-billed Gull	1964	291	251	100	"
Glaucous-winged Gull	1958-1962	270	181	113	Drent et al. 1964 Vermeer, 1963

Although the Glaucous-winged Gull fledging rate fluctuated yearly from 0.5 to 1.7 fledglings per pair of gulls over a five-year period, the average reproductive success of this coastal species is remarkably similar to that of the two inland breeding species at Miquelon Lake in 1964.

6. THE NESTING HABITAT

6.1 Nesting sites in the area. On the basis of observations on several nesting colonies of gulls in Alberta and Saskatchewan, it was concluded that California and Ring-billed Gulls preferred to nest on islands which had low and sparse plant cover in the spring. In 1964, when I arrived on island A on May 7, egg-laying was already advanced. Most of the nests of both species were found where the dead herbaceous cover was short and sparse. On April 25, 1965, when the island was only half covered with snow, both species were observed to settle where the snow remained and where the least vetetation occurred. On April 30, when the snow had disappeared, I stripped the herbaceous cover from one and a half acres near the Ring-billed Gull nesting locality. The next morning many Ring-billed Gulls had established territories in the clearing. From the result of the experiment and other observations, it appeared that Ring-billed Gulls and also the California Gulls, preferred to nest where the vegetation was low and sparse.

The avoidance of dense herbaceous or shrub cover around the nests may be an anti-predator mechanism. Since the plumage of the nesting gulls does not blend well with the surroundings, the bird will be conspicuous to a predator. If it nests in the open, it will have an opportunity to see an arriving predator, whereas if it nests in dense herbaceous cover, its sighting of approaching predators would be hindered. Therefore, it is advantageous for gulls to nest in the open. In gull colonies, where many birds can watch in all directions, a predator has less chance of arriving unseen and an alarm call, given by one bird, will alert all birds in the colony. W. R. Salt (pers. comm.) has suggested that gulls may require sites free of the obstructions to

take flight rapidly. Galucous-winged Gulls on Mandarte Island, which had territories at the edge of dense shrubbery, nested underneath the shrubbery. Tunnels 3 to 10 feet long and covered with vegetation connected these nests with the open meadows. At the approach of the observer, the gulls would take flight from the tunnel entrance. Intraspecific competition for nesting sites alone did not appear to cause Glaucous-winged Gulls to nest in such situations, as areas in the open meadows were still available. It may be that the relaxed predator pressure on the gulls there as compared to that on the inland nesting California and Ring-billed Gulls was partly responsible for this type of nesting behaviour.

The California Gulls nested chiefly at the peripheries of both islands A and B and on the most elevated and boulder-strewn area on island A. The Ring-billed Gulls nested on flat and elevated terrain.

The choice of the nest-site is also partly determined by the locality where the birds nested previously. In 1964, six adults of each species were colour-banded on island B. In 1965, four of the banded adults (two California and two Ring-billed Gulls) were observed. Each one occupied the same territory as in the previous year. One banded Ring-billed Gull had its nest on the exact spot where it nested in 1964. One of the functions of nest-site faithfulness may be to ensure that the gulls return to breed where successful breeding has occurred. It was noted that on some low-lying localities on the islands in Miquelon Lake, vegetative cover was scarce, but no (or relatively few) gulls nested there. Nest-site faithfulness may explain the absence of gull nests in these areas. The low-lying areas were the last ones to emerge from the lake, hence gulls may not have occupied these areas as yet.

In 1965, 65 pairs of California Gulls started to nest in region C (Fig. 2) by the middle of May. This was 33% of all the California Gulls which bred at Miquelon Lake that year. The gulls may have moved to region C in response to disturbance on islands A and B. One colour-banded California Gull which had a nest on island B earlier in May was later found nesting in region C. Forty-seven clutches were initiated on peninsula C_4. All of these were destroyed within 14 days of the commencement of the first clutch. Tracks on the peninsula and the large rectangular bites in the egg shells suggested that they had been destroyed by coyotes (*Canis latrans*). The remaining 18 clutches were located on island C_1. By May 30 the lake level had fallen to a point where this island became connected to the mainland. Within a week, coyotes had destroyed all the clutches.

An inhabitant of the town of Lac la Biche related to me that a coyote remained on one of the large islands in Lac la Biche after the ice had melted in the spring. A large colony of California Gulls, located on the island, did not produce any young as a result of the coyote's predation. That coyotes eat birds as well as eggs has been shown by Murie (1940). He found that 5% of 5,086 scats of coyotes in Yellowstone National Park contained birds, including ducks, geese and grouse. An investigation by the Bureau of Biological Survey over a five-year period in western North America showed a 6% frequency of bird remains (other than poultry) in about 30,000 coyote stomach examinations (Young, 1951). These observations suggest that islands are selected as nesting habitats by gulls because they are relatively free of mammalian predation. Emlen et al. (1966) observed that in a Ring-billed Gull nesting unit of 1000 nests situated on a peninsula in Michigan, only a few chicks survived beyond the second day as a result of raccoon predation.

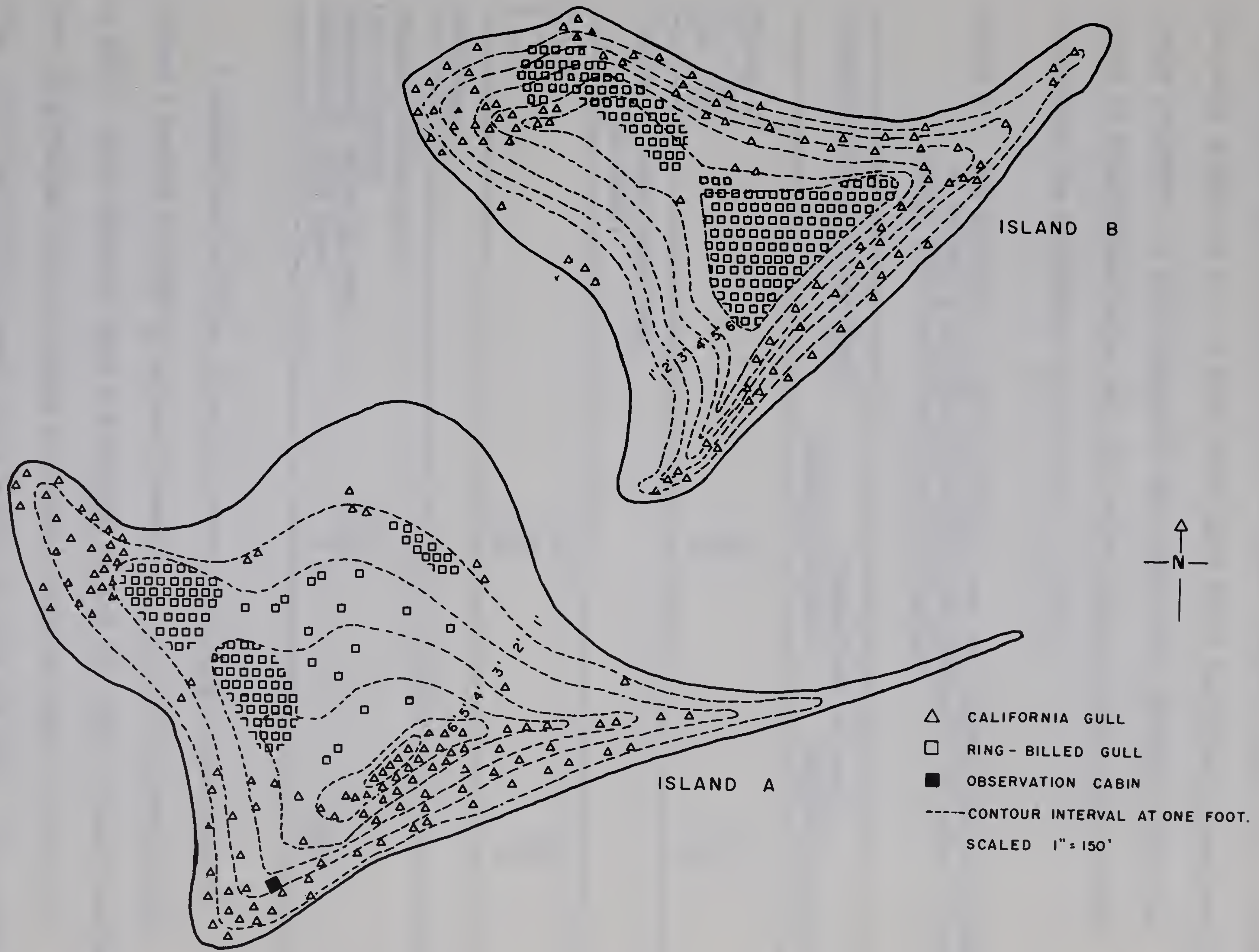
The large majority of the eggs and young died of parental neglect induced by the predator's presence.

Colonial larids in temperate North America are chiefly confined to islands and marshes, while in Europe it is not uncommon to find gulls nesting successfully on sand dunes along the coasts (Goethe, 1956; Kruuk, 1964; Tinbergen, 1953). This habit may be a relatively recent phenomenon developing through the lack of terrestrial predators.

6.2 Interspecific differences in the nesting habitat. Early in 1965, when the island was still covered with snow, many California and Ring-billed Gulls appeared to have changing and very flexible territories. Although intraspecific clashes took place, no interspecific conflict was observed when the territories of the two species were being established. When California Gulls moved into Ring-billed Gull territories, the California Gulls were not evicted by the Ring-billed Gulls. Moynihan (1956) studied the behavioural interactions between California and Ring-billed Gulls at Dog Lake, Manitoba. He observed that Ring-billed Gulls away from their territories usually retreated from California Gulls; only very rarely did a Ring-billed Gull on its territory make a brief and hesitant attack on an intruding California Gull. My observations made at Miquelon Lake agree with these. The Ring-billed Gulls at Miquelon Lake retreated when California Gulls approached them at the time of territorial establishment; hence, the presence of the California Gulls seemed to limit the area in which Ring-billed Gulls were allowed to nest.

Fig. 12 shows the distribution of nests of the California and Ring-billed Gulls on islands A and B at Miquelon Lake in 1964. It can be seen in Fig. 12 and Table 23 that the California Gulls generally nested in proximity to the water and in relatively sloping areas. The Ring-billed Gulls nested farther away from the water and in relatively flatter

Fig. 12. Distribution of California and Ring-billed Gull nests on islands A and B in 1964.


ISLAND B
ISLAND A
1
2
3
4
5
6
N
△ CALIFORNIA GULL
□ RING - BILLED GULL
■ OBSERVATION CABIN
-----CONTOUR INTERVAL AT ONE FOOT.
SCALED 1" = 150'

areas (Fig. 13). More California Gulls than Ring-billed Gulls nested in localities with boulders, which provided lookouts (Table 23 and Fig. 14). The area which was 4 to 6 feet above lake level was chiefly composed of large boulders. A few California Gull nests were situated among the nests of Ring-billed Gulls but only where large boulders were nearby to provide the California Gulls with a look-out.

Table 23. The location of 206 California and 265 Ring-billed Gull nests on island A in 1964 in relation to proximity of water, elevation above lake level and type of topography.

Proximity of water (in feet)	Percentage of nests	
	California Gull	Ring-billed Gull
Within 75	68	27
75 - 150	32	63
150 - 225	0	10
Elevation above lake level (in feet)		
0 - 2	60	16
2 - 4	14	78
4 - 6	26	6
Topography		
Boulder-strewn area (rel. sloping)	34	4
Relatively sloping area	61	6
Relatively flat area	5	90

A comparison of Figs. 12 and 15 shows that Ring-billed Gulls on island A nested in 1965 in an area occupied solely by California Gulls in 1964. When Miquelon Lake was visited on May 20, 1967, it was observed that Ring-billed Gulls occupied localities near the water on island B (Fig. 16) in which California Gulls nested in 1964 and 1965. The nesting of the Ring-billed Gulls in localities previously occupied by California Gulls was possible through the absence of the latter species from these areas. From observations that California Gulls nest among Ring-billed

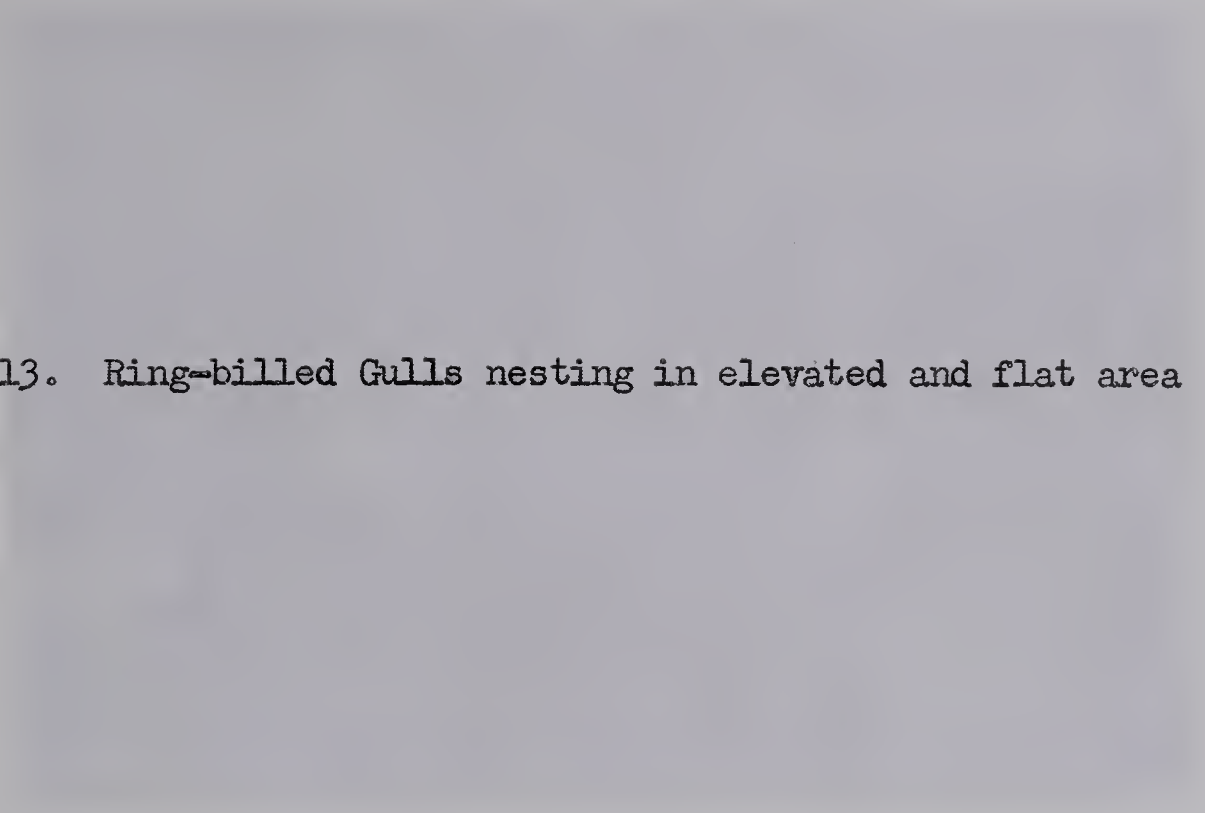


Fig. 13. Ring-billed Gulls nesting in elevated and flat area

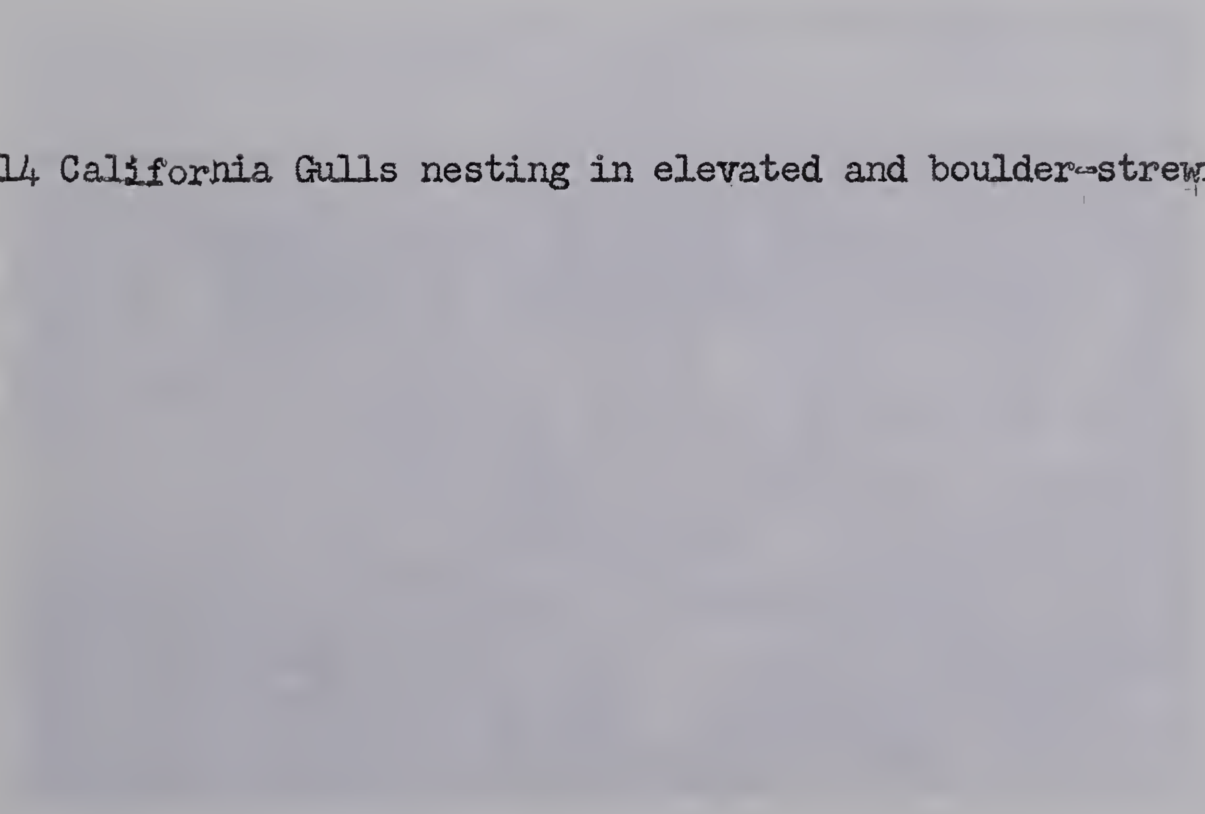


Fig. 14 California Gulls nesting in elevated and boulder-strewn area

Fig. [illegible] and [illegible]
[illegible]

Fig. 15. Distribution of California and Ring-billed Gull nests on island A in 1965

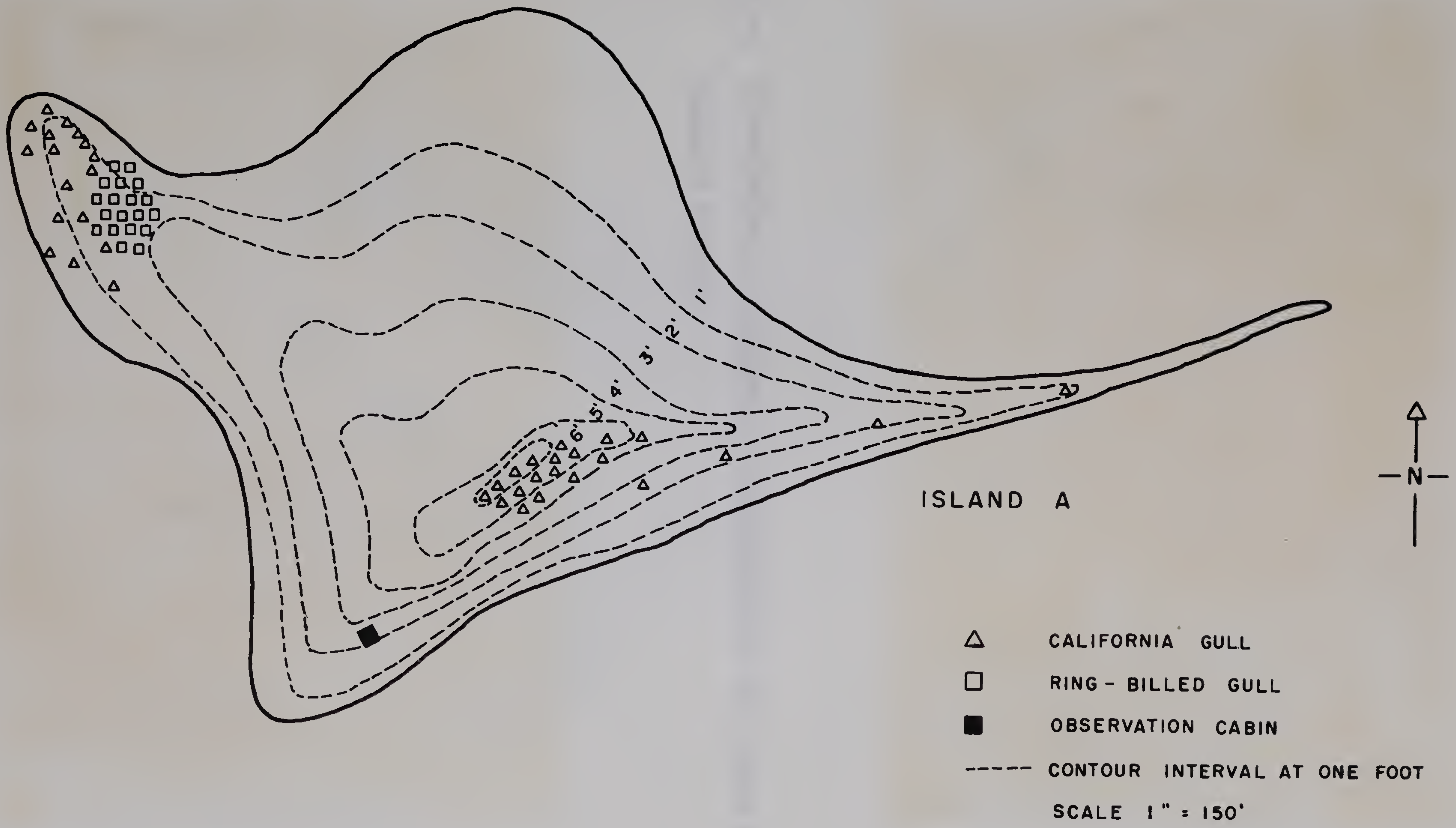
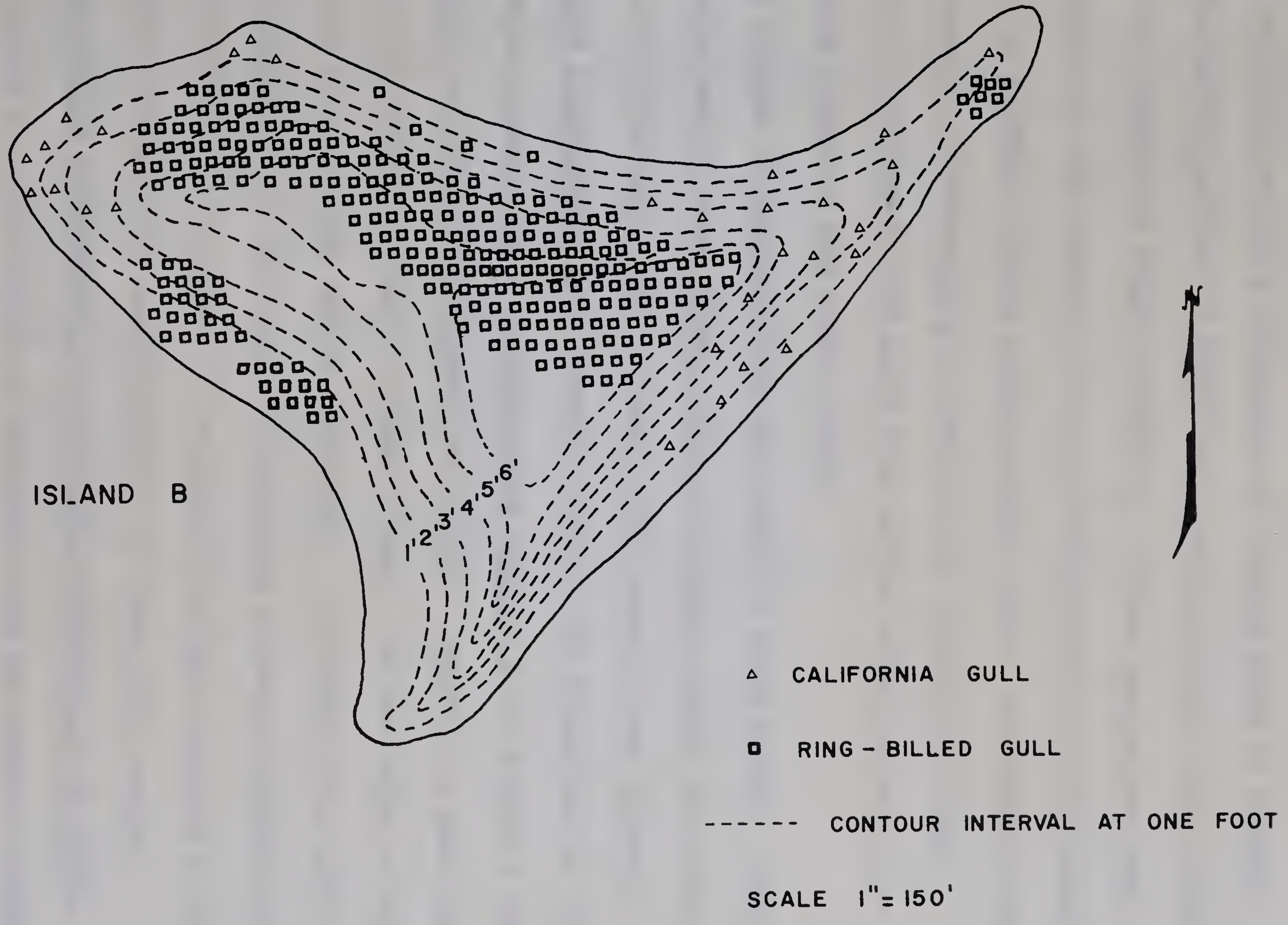

ISLAND A
N
1'
2'
3'
4'
5'
6'
△ CALIFORNIA GULL
□ RING - BILLED GULL
■ OBSERVATION CABIN
----- CONTOUR INTERVAL AT ONE FOOT
SCALE 1" = 150'

Fig. 16. Distribution of California and Ring-billed Gull nests on island B in 1967


ISLAND B
1'
2'
3'
4'
5'
6'
N
△ CALIFORNIA GULL
□ RING - BILLED GULL
------ CONTOUR INTERVAL AT ONE FOOT
SCALE 1" = 150'

Gulls and Ring-billed Gulls nest in habitat previously occupied by California Gulls, it appears that both species can nest in the same island habitat.

The relative locations and degree of overlap found by various workers in nesting habitat of California and Ring-billed Gulls nesting together on islands are shown in Table 24. Either species may nest at the margins, in the centre, at low or elevated areas on the islands, but there is generally little overlap between them. The moderate amount of interspecific intermingling of nests at the Honey Lake colony, California is ascribed to the small size of the island on which the gulls nested (Johnston and Foster, 1954).

Both species at Miquelon Lake nest still on level ground. Black-headed Gulls nest in dunes (Kruuk, 1964; Patterson, 1965), in marshes, or on islands (Ytreberg, 1956). Smith (1966) reports that Glaucous Gulls (Larus hyperboreus) nest commonly both on the ground and on cliff ledges, while Iceland Gulls (L. glaucoides kumlieni) and Thayer's Gulls (L. thayeri) nest almost exclusively on cliffs. However, in some cases the latter two species do nest on level ground. The Mew Gulls in North America nest both in trees and on the ground. In summary, the interspecific differences in the choice of nest-site between California and Ring-billed Gulls do not appear to be significant when compared to the intraspecific variation in nesting habitat of other gull species.

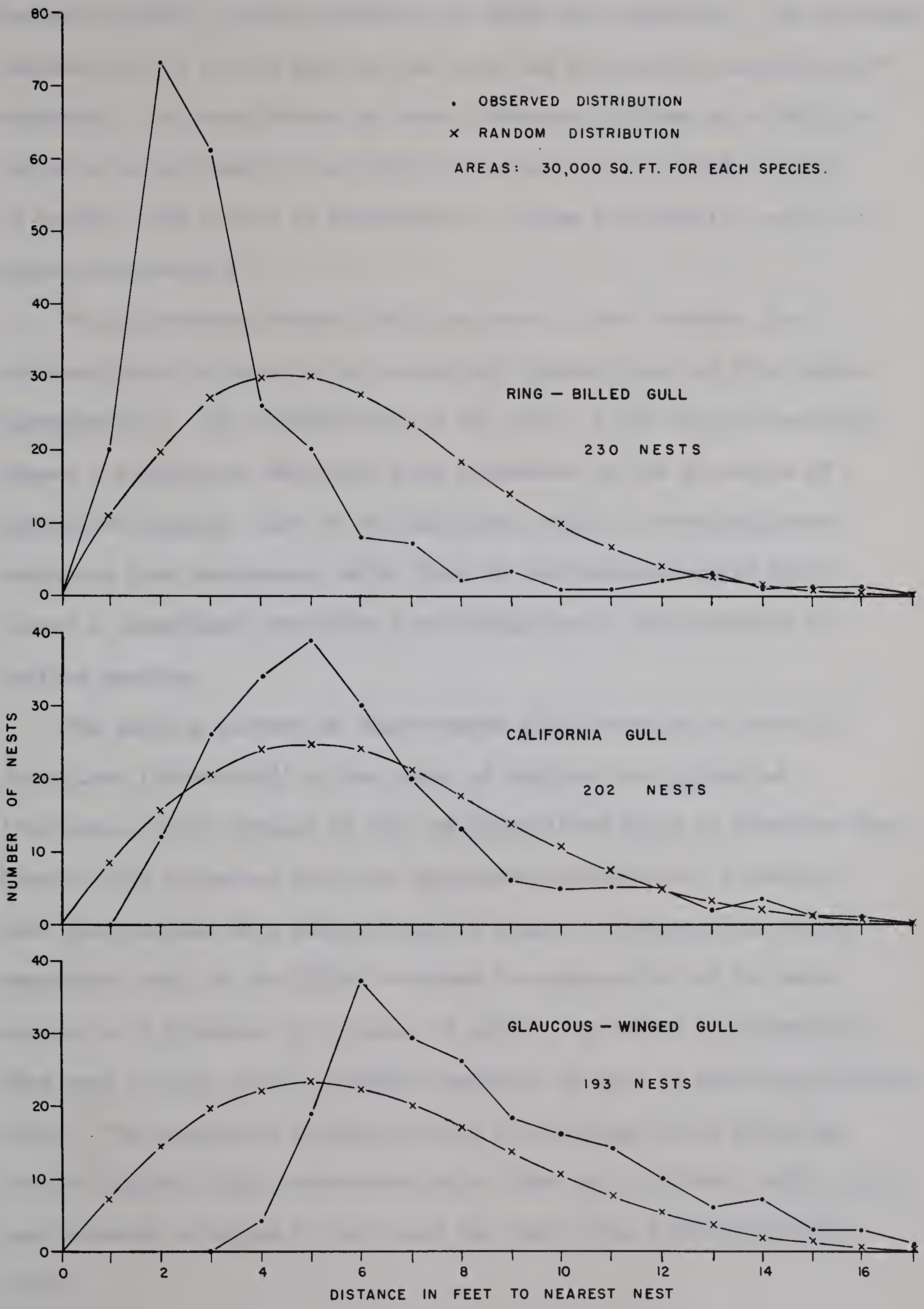
6.3 Interspecific differences in the spatial distribution of nests.

Fig. 17 depicts the distribution of distances from the nearest neighbor of 230 Ring-billed and 202 California Gull nests in a 30,000 square feet area for each species on island A at Miquelon Lake. A similar distribution for 193 Glaucous-winged Gull nests in an area of 30,000 square feet on

Table 24. Location and degree of overlap in the nesting habitat of California and Ring-billed Gulls at different geographical locations.

Authority	Geographical location	Species	Nesting location on island				Degree of overlap in nesting habitat		
			periphery	centre	low	elevated	none or little	lightly	moderately
Bent, 1921	Big Stick L. Saskatchewan	California Gull	+	-	+	-	-	+	-
		Ring-billed Gull	-	+	-	+	-	+	-
Hanson, 1963	Columbia R. Washington St.	California Gull	-	+	-	+	+	-	-
		Ring-billed Gull	+	-	+	-	+	-	-
Johnston and Foster 1954	Honey Lake California	California Gull	-	+	-	+	-	-	+
		Ring-billed Gull	+	+	+	+	-	-	+
This study	Miquelon L. Alberta	California Gull	+	-	+	+	+	-	-
		Ring-billed Gull	-	+	-	+	+	-	-

Fig. 17. Distribution of distances between nests in three gull species


• OBSERVED DISTRIBUTION
× RANDOM DISTRIBUTION
AREAS: 30,000 SQ. FT. FOR EACH SPECIES.
RING — BILLED GULL
230 NESTS
CALIFORNIA GULL
202 NESTS
GLAUCOUS — WINGED GULL
193 NESTS
NUMBER OF NESTS
DISTANCE IN FEET TO NEAREST NEST
0
10
20
30
40
50
60
70
80
0
2
4
6
8
10
12
14
16

Mandarte Island, British Columbia, is shown for comparison. The distances between the top of the rims of each nest and its nearest neighbour were measured. The distribution of these distances is shown with the distribution which would be expected if the nests were spaced entirely at random. The method of obtaining the random distribution curves is given in Appendix 2.

The Clark-Evans method (1954) was used to test whether the observed distributions in the three gull species departed from random distributions. The distribution of the nests of the Ring-billed Gulls showed a significant deviation from randomness in the direction of aggregated spacing, that of the California Gulls a non-significant deviation from randomness, while that of the Glaucous-winged Gulls showed a significant deviation from randomness in the direction of uniform spacing.

The nesting pattern of Black-headed Gulls breeding on dunes at Ravenglass (Cumberland) in the north of England was aggregated (Patterson, 1965) similar to that of Ring-billed Gulls at Miquelon Lake. Kruuk (1964) suggested that the aggregated distribution of nests in this Black-headed Gull colony allows a number of behavioural defense mechanisms such as the flight response to alarm calls and the mass attacks on a predator by a number of gulls. He showed experimentally that such attacks greatly reduced predation on eggs by Crows and Herring Gulls. The aggregated nesting pattern of the Ring-billed Gulls may protect against large predaceous gulls, like the California Gulls, which were commonly observed to prey upon the very young Ring-billed Gull chicks.

The tendency toward uniform spacing of Glaucous-winged Gull nests may result from the strong territoriality observed in this species. It was shown by a nest-moving experiment (Vermeer, 1963) that territorial agression kept this species from nesting as close as California and Ring-billed Gulls.

Since the Black-headed Gulls in the English dunes nest in a aggregated pattern similar to that of the Ring-billed Gulls, it can be concluded that this type of nesting pattern is not a special adaptation to inland conditions.

7. FOOD HABITS

7.1 Food habits during the breeding cycle. Table 25 shows the frequency and volume per cent of identifiable food items collected from esophagi and regurgitations of adults and chicks of both species during May, June and July of 1965. The main items in the diet of the Ring-billed Gulls changed from plant foods in May to insects in June, and then to refuse from garbage dumps and other sources of disposal in July. The data for the California Gulls indicated that no food group dominated in May, insects dominated in June, refuse in July. The plant foods in May for both species consisted mainly of oats, barley and wheat. This may not present a normal picture of the May diet, since the spring season of 1965 was late and other food sources may have been limited. The food of chicks in June and July was similar to that of the adults.

Rodents were an important supplementary food source for both gull species and throughout the whole breeding season. The importance of rodents was evident in an analysis of pellets of the adult gulls (Table 26). The pellets were relatively pure, in that more than 90% of them contained only one food item.

In 1965, only 13% of 39 pellets of Ring-billed Gulls collected from April 30 to May 19 contained Microtus pennsylvanicus. Of 36 pellets of Ring-billed Gulls collected on May 20 in that year, 56% contained mice, mostly M. pennsylvanicus, but including a few Peromyscus maniculatus. Mice must have become suddenly available around May 20 in that year.

%

Table 25. Frequency and volume of identifiable food items from esophagi and regurgitations of adult and chick California and Ring-billed Gulls collected in May, June and July of 1965 at Miquelon and Beaverhill Lakes

Location	Month	No. of regurgitations and esophagi with food				Food items	Frequency and volume of food items in per cent							
		California Gull		Ring-billed Gull			California Gull				Ring-billed Gull			
							Adults		Chicks		Adults		Chicks	
		Adults	Chicks	Adults	Chicks		Freq.	Vol.	Freq.	Vol.	Freq.	Vol.	Freq.	Vol.
Miquelon Lake	May	15	0	12	0	Plants	33	28			75	68		
						Arthropods	7	0			25	6		
						Amphibians	0	0			0	0		
						Bird remains	20	18			0	0		
						Rodents	27	30			17	10		
						Refuse	27	24			17	16		
Miquelon Lake	June	60	25	21	8	Plants	3	1	4	0	14	5	13	8
						Arthropods	50	39	52	42	57	54	63	50
						Amphibians	2	1	4	2	0	0	0	0
						Bird remains	33	21	36	22	5	2	13	7
						Rodents	18	23	20	24	19	29	25	21
						Refuse	18	15	12	10	10	10	25	14
Miquelon and Beaverhill Lakes	July	14	18	13	16	Plants	14	6	0	0	0	0	13	10
						Arthropods	14	4	12	2	15	4	13	1
						Amphibians	0	0	0	0	0	0	0	0
						Bird remains	0	0	12	11	0	0	6	8
						Rodents	21	24	22	28	23	20	19	15
						Refuse	71	66	61	59	85	76	69	66

Table 26. Percentage frequency of different food items in 155 pellets of California and 250 pellets of Ring-billed Gulls collected in May and June of 1965

Food items	Percentage of food items California Gull	 Ring-billed Gull
Plants	17	31
Arthropods	13	20
Bird remains	37	7
Rodents	48	61
Refuse	5	3
Other food (fish, amphibians, weasel)	7	3

In 1966, four of five Ring-billed Gulls collected in mid-April contained food items. These were, in all cases, the remains of M. pennsylvanicus. The spring of 1966 was probably exceptional, as the vole populations were at extremely high levels. More than 90% of the gull pellets collected in the last week of April and the first week of May, 1966, contained remains of this rodent (Table 27).

Table 27. Percentage frequency of food items in 55 Ring-billed and 25 California Gull pellets collected respectively on April 29 and May 7, 1966.

Food items	Percentage of food items California Gull	 Ring-billed Gull
Grain	0	5
Arthropods	4	5
Microtus pennsylvanicus	100	91
Peromyscus maniculatus	8	3
Citellus richardsonii	0	3

The annual difference in appearance of rodents in the gull diet may reflect not only a fluctuation in numbers of these animals between the years, but also their availability.

Plant foods, chiefly grain, were more important in the diet of the Ring-billed Gulls than in the California Gulls in May, 1965. Of 39 pellets of the Ring-billed Gulls collected from April 30 to May 19 in that year, 82% were composed of grain. Of 36 pellets collected on May 20 in that year, 37% contained grain. The grain diet declined probably as a result of the sudden availability of *Microtus pennsylvanicus* to the Ring-billed Gulls on May 20. The difference in the early spring diet of both species between 1965 (chiefly grain) and 1966 (chiefly rodents) suggests the opportunistic feeding habits of both gull species.

Arthropods were the main food source for both species of gulls in June. Table 28 shows the relative importance of the different groups of arthropods in the diet of the two gull species. In both California and Ring-billed Gulls, carabids and coenagrionids were most frequently occurring arthropods. There are no apparent interspecific differences in the proportions of arthropods taken by the two gull species.

Table 28. The relative importance of specific arthropods in esophagi and regurgitations of 40 California and 25 Ring-billed Gulls in 1965

ARTHROPODS	Percentage of food items California Gull	 Ring-billed Gull
Arachnida		
Lycosidae (adults)	2.5	0
Crustacea		
Anostraca (adults)	0	12
Malacostraca (Gammarus lacustris)	2.5	0
Insecta		
Siphonaptera	0	4
Hemiptera		
Corixidae (adults)	4	0
Reduviidae (adults)	2.5	0
Coleoptera		
Carabidae (adults)	60	48
Scarabaeidae (adults)	10	4
Curculionidae (adults)	5	4
Dytiscidae (adults)	2.5	0
Hysteridae (adults)	2.5	0
Elateridae (adults)	2.5	0
Trichoptera	0	8
Plecoptera	2.5	0
Lepidoptera		
Noctuidae (larvae)	2.5	4
Pieridae (adult and pupae)	0	4
Diptera		
Tipulidae (larvae)	2.5	0
Therevidae (pupae)	0	4
Tabanidae (larvae)	2.5	0
Tachinidae (pupae)	0	4
Sarcophagidae (larvae)	5	0
Chironomidae (larvae)	2.5	12
Hymenoptera		
Ichneumonidae (pupae)	0	4
Sphecidae (adult)	0	4
Odonata		
Coenagrionidae (nymphs)	22.5	32
Ephemoptera (adults)	2.5	4
Orthoptera		
Acrididae (nymphs)	2.5	4

The appearance of insects in the gull diet closely coincided with the onset of hatching of the chicks. Most of the insect-containing regurgitations of adults and chicks dated from the first week of June, 1965 when carabid beetles made up the majority of insects. The damselfly nymphs appeared in the gull diet in mid-June of that year, but in the previous year they were observed to be numerous in regurgitations of adults and chicks in the first week of June. The late disappearance of snow and ice in 1965 probably delayed the appearance of the damselfly nymphs in that year.

It was seen that refuse dominated in the diet of both species in July (Table 25). The rodents may have formed a more substantial part of the July diet in the past before refuse became available to the gulls as a result of an increasing human population. In August and September, large concentrations of adults and chicks were observed on city refuse dumps, indicating that the gulls use refuse extensively as a source of food after departure from the breeding grounds.

Although fish seemed to be a relatively unimportant food of the gulls at Miquelon Lake (Tables 25 and 26) the infection of gull chicks with helminths acquired from fish (section 8), showed that fish are common food items in the gull diet. During a visit to a California gull colony at Lac la Biche in August, 1966, I observed many gull regurgitations containing fish scales. Lewis (1941) stated that the food of the Ring-billed Gulls in colonies on islands in the St. Lawrence River consisted chiefly of fish. Fish may also form a substantial part of the gull diet during the autumn migration. W. Turner (pers. comm.) observed numerous California and Ring-billed Gulls swimming about and feeding on kokanee (Oncorhynchus nerka) and chub (Mylocheilus caurinus) when these fish arose to the surface in Kootenay Lake in British Columbia in the autumn of 1965.

7.2 Interspecific differences. From the literature on the food and feeding habits of the California and Ring-billed Gulls in the spring and summer, it appears that the two species share many food items. This fact is born out in the present study.

The extensive grain diet observed in the Ring-billed Gulls in the spring of 1965 may indicate a preference for feeding in a terrestrial habitat. Munro (1936) also found that grain predominated in Ring-billed Gull pellets collected in May, 1934, at Bittern Lake, 15 miles from Miquelon Lake.

Rothweiler (1960) identified various insect families in stomach samples collected in Montana. His results show a preponderance of carabids in the diet of both gull species. In addition corixids and scarabids were important in the diet of California Gulls, whereas gryllids, acridids, curculionids and muscids were important to Ring-billed Gulls.

At Miquelon Lake, tiger salamanders (Ambystoma tigrinum) occurred three times in the food sample of California Gulls, but not at all in that of Ring-billed Gulls. Rothweiler (1960) also found none in Ring-billed Gulls, but they occurred in 10% of the investigated California Gull stomachs. Hence, California Gulls appear to feed on tiger salamanders more than do Ring-billed Gulls.

Bird remains were at least four times more abundant in the California than in the Ring-billed Gull pellets. Table 29 shows the frequency of different bird and egg shell remains in esophagi, regurgitations and pellets of the gulls in 1965.

Table 29. Frequency of different bird and egg shell remains in esophagi, regurgitations and pellets of California and Ring-billed Gulls during May and June, 1965.

Type of bird remains	Frequency of: 45 bird remains in California Gull	Frequency of: 12 bird remains in Ring-billed Gull
gulls	25	3
duck	5	0
coot	3	0
grebe	2	0
passerine	1	5
unidentified	9	4

Type of egg shell remains	Frequency of: 50 egg shell remains in California Gull	Frequency of: 9 egg shell remains in Ring-billed Gull
gulls	6	5
duck	35	2
coot	4	0
grebe	2	0
passerine	0	0
unidentified	3	2

California Gulls preyed more on the very young gulls and waterfowl while passerine birds were relatively more important in the Ring-billed Gulls' diet.

The data on egg shell remains show that California Gulls preyed mostly on duck eggs, whereas Ring-billed Gulls apparently ate relatively more gull eggs. The fragments were too small to make species identification possible but direct observations in the colony showed that Ring-billed Gulls ate their own eggs in 1965.

The ducklings identified from California Gull regurgitations were Gadwall, Lesser Scaup and Bufflehead (_Bucephala albeola_). On seven occasions I observed California Gulls consuming entire broods of ducklings at Miquelon Lake. The broods involved were those of a Mallard, a Pintail, a Gadwall, and four Lesser Scaup. I also watched a coot chick being taken by a California Gull in a pond adjacent to Miquelon Lake. The data indicate that California Gulls prey more heavily on waterfowl than do Ring-billed Gulls.

In 1964 and 1965 the hatching success of early nesting ducks, such as Pintails and Mallards, on islands A and B was low as compared to that of late nesting species such as Lesser Scaup and Gadwall. This may have resulted from the disturbance I caused in checking gull nests, and the consequent exposure of the eggs to gull predation when left uncovered in the sparse vegetation by the departing duck. Hatching success of late nesting ducks was good in 1964, since vegetation then prevented exposure of the nests and the ducks had become accustomed to my presence. A total of 67 Lesser Scaup and 29 Gadwall nests were found on islands A and B in 1964. The hatching success of the clutches of both duck species was 90%. However, the fledging success of all ducks nesting on the islands was probably low because of predation by California Gulls. It is unlikely that any duckling survived its fourth day of life. As soon as a hen with her ducklings entered the water the gulls would pursue them, devouring the entire brood, usually within ten minutes. If a particular gull did not swallow a duckling fast enough in the air, another gull would take the prey and the spectacle assumed the appearance of a fast ball game. I observed on two occasions that when the brood of a scaup was reduced to one, a second female scaup, without a brood, would come to the defence of the lone duckling. Although both hens tried to defend the duckling placed between them they were unsuccessful. On July 30, 1964, when there were only ten adult California Gulls left on island A, a scaup with nine ducklings took to the water and lost her brood within a few minutes. It is obvious that a few gulls can destroy substantial numbers of ducklings in a very short time. On two occasions I observed for a few hours a Pintail brood and a Mallard brood moving about on the island. The gulls did not attack the ducklings, although the latter appeared conspicuous to me. The gulls appeared to ignore

the ducklings completely. As soon as they went into the water, the gulls pursued them. The cryptic colouration of the young ducklings may have protected them on land but not in the water where they became conspicuous.

Duck eggs formed the most substantial part of the egg predation by the California Gull at Miquelon Lake. Odin (1957) found that within a two-mile radius of the nearest California Gull colony at Farmington Bay, Utah, 18.3% of 2997 duck and coot eggs were destroyed by the California Gulls. Wingfield (1951) in a waterfowl study, also in Utah, calculated that 8% of all waterfowl eggs were destroyed by California Gulls. In both studies predation was heaviest on nests which were poorly concealed. Wunder (1949) in a study on predation on waterfowl at Farmington Bay found the California Gull responsible for the destruction of 11.3% of 834 waterfowl eggs. In the Miquelon Lake study, of 287 California Gull esophagi, regurgitations and pellets, 35 contained duck shells. This is a 12% occurrence compared with a 13% occurrence of duck egg shells in the California Gulls collected by Odin. By this calculation, duck eggs appear to be utilized by gulls to the same extent at Miquelon Lake, Alberta, and at Farmington Bay, Utah.

Anderson (1965) in California, Rothweiler (1960) in Montana, and Williams and Marshall (1938) in Utah showed that California Gull predation on waterfowl nests was less than 5%. The amount of California Gull predation thus appears to vary from one region to the next, probably depending on such factors as the amount of cover in which duck nests are located, proximity of gull colonies, availability and abundance of other food sources, location or feeding area where the gulls were collected for food analysis and extent of human disturbance.

California Gull predation on young waterfowl has been reported from several sources. Odin (1957) observed a week-old Pintail and a 10-day old Redhead (*Aythya americana*) duckling being taken by California Gulls. He also reported a seven-day-old Avocet (*Recurvirostra americana*), a young coot and duck down in California Gull stomachs. Odin considered young waterfowl which had reached three-quarters of their growth to be safe from California Gull predation. Greenhalgh (1952) found seven ducklings in 184 California Gull stomachs collected at two locations in Great Salt Lake. Chura (1962) saw a California Gull capture a Mallard duckling held in an enclosure. The gull swallowed the duckling, which was 23 days old and weighed 260 grams, whole. Anderson (1965) observed the taking of ducklings, a young Eared Grebe and a newly hatched coot. Greenhalgh (1952) and Cottam (1945) reported California Gulls preying upon ducks (age not specified) incapacitated by botulism. Behle (1958) mentions the taking of crippled and sick ducks, young pelicans and cormorants.

J. Guay (pers. comm.) and Wolford (1966) observed that the Ring-billed Gull was a predator on the eggs of Franklin Gulls (*Larus pipixcan*) and Black-crowned Night Herons (*Nycticorax nycticorax*) respectively, in Alberta. The Ring-billed Gulls apparently ate relatively more passerine birds than the California Gulls (Table 30), but on no occasion at Miquelon Lake were young waterfowl observed in their food.

The frequency of different rodent species in gull pellets collected in May and June of 1965 is shown in Table 30.

Table 30. Percentage frequency of different rodent species in 74 California and 152 Ring-billed Gull pellets containing rodents collected in May and June, 1965

Rodent species	Percentage of frequency of rodent species California Gull	Ring-billed Gull
Ondatra zibethicus	3	0
Citellus richardsonii	53	17
Thomomys talpoides	13	18
Microtus pennsylvanicus	27	52
Peromyscus maniculatus	4	13

It is evident that California Gulls concentrated more on the larger rodents, while the Ring-billed Gulls fed more on mice. From Anderson's (1965) analysis of mammalian remains in gull stomachs in California, it appeared that Ring-billed Gulls ate more mice, while the California Gulls took larger mammals. Interspecific differences in size of the gulls may account in part for the size of mammals taken (Appendix 3). Recher (1966) showed that larger-sized species of shorebirds tend to feed upon larger prey organisms.

Hansen (cited by Behle, 1958) reported that California Gulls congregated in irrigated fields in the spring and ate pocket gophers which had been forced from their burrows by water. Mr. Webster, a resident in the vicinity of Miquelon Lake, stated that he saw a Ring-billed Gull killing and swallowing a pocket gopher. Dutcher (cited by Behle, 1958) reported that California Gulls fed on mice which were forced from their holes by irrigation water. Cottam (1945) mentioned that California Gulls followed the road, feeding on mammals hit by automobiles. Munro (1936) said that

it was a common sight to see Ring-billed Gulls tearing at carcasses of ground squirrels which were killed on the road. It appears that gulls take their rodent prey either dead or alive.

From the above observations, it can be concluded that the two gull species have slightly different food niches.

Although no quantitative food study of the California and Ring-billed Gulls from the coastal wintering grounds is known to me, it appears that fish (Bartholomew, 1942; Norris-Elye, 1945) and marine invertebrates (Meyerriecks, 1965; Wales, 1926) may form a substantial part of the diet of these gulls. Quantitative food studies on the Herring Gull show that the diet of inland nesting populations can be composed chiefly of rodents and insects (in Kalmytskaya, Russia - Minoranskii, 1963) while coastal populations feed mainly on fish and marine invertebrates (Barents Sea, Russia - Belopolskii, 1957; coastal western Europe - Harris, 1965; coastal eastern North America - Mendall, 1935 and Pimlott, 1953). Ishunin (1964) found that the diet of inland nesting Black-headed Gulls at Lake Sivash, Russia consisted chiefly of rodents. Although food studies of inland nesting gulls are few, a diet chiefly composed of rodents and insects may be common for other gull populations nesting inland.

8. THE HELMINTH FAUNA

8.1 General. Little is known of the helminth fauna of California and Ring-billed Gulls. Young (1950), on the California coast, found *Tetrabothrius lari*, *Paricterotaenia porosa* and *Hymenolepis californicus* in both California and Ring-billed Gulls. Brown (1950) found only two helminth species, *H. californicus* and *P. porosa*, in the digestive tracts of California Gulls in Utah.

The extensity of helminth infections in California and Ring-billed Gulls at Miquelon and Beaverhill Lakes in 1964 and 1965 is shown in Table 31. It can be seen that the helminth fauna of both gull species at Miquelon Lake consists of the same species, with the exception of *Renicola* sp., *Cotylurus erraticus*, *Austrobilharzia* sp., and *Schistocephalus solidus*, which were found in Ring-billed Gulls, only. If the host sample had been larger, these helminths might also have been found in California Gulls.

8.2 Tremodes. In 1964, as in 1965, *Plagiorchis elegans* was the most numerous trematode in each gull species. The total extensity of infection with *P. elegans* in Ring-billed Gulls was significantly greater than in California Gulls. The intensity of infection with *P. elegans* was also significantly greater in the Ring-billed Gulls. In 1965, the average number of *P. elegans* per Ring-billed Gull was 11.5 as compared to 6.5 in California Gulls. The average number of *P. elegans* per adult Ring-billed Gull declined from 15 in May to between 6 and 4 in June and July of 1965. Only six adult California Gulls contained *P. elegans*, four in May, and two in July. The intensity of *P. elegans* for both species was greatest in May. Styczyńska - Jurewicz (1962) found metacercariae

Table 31. Extensity of helminth infection recorded from California and Ring-billed Gulls

	California Gull					Ring-billed Gull				
Year	Adults 1964	Adults 1965	Chicks 1964	Chicks 1965	Foster[a] chicks 1965	Adults 1964	Adults 1965	Chicks 1964	Chicks 1965	Foster[b] chicks 1965
No. of birds examined	13	21[c]	30	8	10	13	23[c]	30	10	10
Trematodes										
Plagiorchis elegans	0	7	13	2	4	0	18	20	9	3
Diplostomum spathaceum	0	1	3	0	0	0	11	1	0	0
Echinostoma revolutum	0	0	1	0	0	1	2	3	0	0
Echinoparyphium sp. (cf. *recurvatum*, *flexum*)	0	0	1	0	0	0	1	4	0	1
Cotylurus erraticus	0	0	0	0	0	0	1	1	0	0
Renicola sp.	6	-	0	-	-	0	-	0	-	-
Austrobilharzia sp.	0	-	0	-	-	1	-	0	-	-
Cestodes										
Diphyllobothrium dendriticum	0	1	0	0	2	1	2	5	0	0
Schistocephalus solidus	0	0	0	0	0	1	0	4	0	0
Paricterotaenia porosa	5[d]	10	5	2	7	4	13	10	2	6
Lateriporus clerci		3		2	3		0		0	6
Hymenolepis californicus	3	5	7	0	0	6	16	10	0	0
Acanthocephala										
Polymorphus sp.	0	0	1	0	0	0	0	1	0	0
Nematodes										
Aprocta turgida[e]	2	0	0	0	0	5	10	0	0	0

a California Gull chicks raised by Ring-billed Gull adults

b Ring-billed Gull chicks raised by California Gull adults

c Due to decomposition, cestodes could not be identified in four of 21 adult California and in one of 23 Ring-billed Gulls

d *Paricterotaenia porosa* and *Lateriporus clerci* were not distinguished in 1964

e Specimens from the Ring-billed Gull identified to species by Dr. R. C. Anderson

- Not looked for in 1965

of P. elegans in mayfly and dragonfly larvae. Since coenagrionids made up one of the major insect food groups for both gull species, the damselfly larvae may have been the main second intermediate host from which the gulls obtained P. elegans.

The total extensity of infection with Diplostomum spathaceum, the second most abundant trematode in the gulls at Miquelon Lake, was significantly greater in Ring-billed Gulls. In 1965, one adult California Gull contained 10 D. spathaceum in May. The average number of D. spathaceum in adult Ring-billed Gulls declined from 9 in May to between 7 and 5 in June and July of 1965. D. spathaceum appeared to have been acquired from freshwater fish. The life cycle of D. spathaceum has been investigated by many authors (Yamaguti, 1958). The greater occurrence of D. spathaceum in Ring-billed Gulls indicates that this bird eats more infected fish than do California Gulls. The occurrence of D. spathaceum in the gull chicks indicates that this species was acquired from fish in the vicinity of the breeding grounds.

Echninostoma revolutum and Echinoparyphium sp. occurred more frequently in Ring-billed Gulls. Cotylurus erraticus was found in Ring-billed Gulls only.

Renicola sp. was found in the kidneys of adult California Gulls only. Five gulls taken in May and one gull taken in June were infected with this species. The average number of Renicola sp. observed in California Gulls was 9 in May and 4 in June of 1964.

Two specimens of Austrobilharzia sp. were found in one adult Ring-billed Gull.

8.3 Cestodes. The total extensity of infection with *Diphyllobothrium dendriticum* was greater in Ring-billed Gulls than in California Gulls. The intensity of *D. dendriticum* in the Ring-billed Gulls averaged three; a total of six worms were found in California Gulls. *Schistocephalus solidus* occurred only in Ring-billed Gulls. The greater occurrence of *D. dendriticum* and *S. solidus* in Ring-billed Gulls indicates that this species eats more infected fish than California Gulls. The occurrence of these cestode species in the gull chicks indicates that, like *Diplostomum spathaceum*, the cestodes were acquired from fish in the vicinity of the breeding grounds.

It can be seen that the extensity of infection with *Paricterotaenia porosa* was similar in both gull species. The average number of *P. porosa* in the Ring-billed Gulls was four as compared to two in the California Gulls; this difference in intensity was significant.

In 1965, *Lateriporus clerci* were found in California Gulls only. None were present in Ring-billed Gulls that year except in the chicks of that species raised by California Gulls. The reason for the greater occurrence of *L. clerci* in California Gulls is not understood. *Gammarus lacustris* is an intermediate host of this cestody species (M. Denny, pers. comm.). The California Gulls, which nest at the peripheries of the islands in Miquelon Lake, may feed more upon *Gammarus lacustris* than the more inland-nesting Ring-billed Gulls.

Hymenolepis californicus occurred significantly more often in Ring-billed Gulls. In 1965 the average number of *H. californicus* in the Ring-billed Gulls was 10, as compared to six in California Gulls; this difference was not significant. Although the extensity of *H. californicus* did not

change significantly from month to month in either gull species, the average intensity of infection with H. californicus decreased significantly over the season. In Ring-billed Gulls the mean number per adult dropped from 17 in May to 6 in June and July 1965. In California Gull adults the average number of H. californicus declined from 12 in May to between 2 and 3 in June and July of 1965. It is therefore possible that the greatest infection with this cestode occurred on or before arrival of the birds at the breeding grounds.

Table 32 shows the geographic variation in infestation of P. porosa and H. californicus in California and Ring-billed Gulls. Since D. dendriticum, S. solidus and L. clerci were not reported in either Brown's or Young's study, they are not included in Table 32.

It can be seen that the P. porosa infection was greater at Miquelon Lake and Beaverhill Lake than in areas reported in the other two studies. In 1965, the extensity of P. porosa in May, June and July was 38%, 71% and 71%, respectively, in adult Ring-billed Gulls, and 33%, 71% and 75%, respectively, in the adult California Gulls. Most of the infection in both gull species seemed to occur on the summer range. Insects may be the main intermediate hosts.

There seems to be considerable variation between the occurrence of H. californicus in the three studies listed in Table 32. Nothing is known about the life cycle of this cestode.

The geographic variation of the cestode fauna may reflect a varying diet from one locality to another. Certain species of fish and Gammarus, as reflected by the infection with D. dendriticum, S. solidus and L. clerci, were more important in the diet of the gulls at Miquelon Lake than in those of these species studied by Brown in Utah and Young in California.

Table 32. Geographic variation of infestation of two cestode species in California and Ring-billed Gulls.

Author Year	Locality collected	No. of gulls analyzed		Percentage frequency of occurrence			
				Paricterotaenia porosa		*Hymenolepis californicus*	
		California Gull	Ring-billed Gull	California Gull	Ring-billed Gull	California Gull	Ring-billed Gull
Young, R.T. 1950	California coast	24 adults	11 adults	4	8	54	36
Brown, W.C. 1950	Salt Lake City, Utah	23 adults	-	9	-	61	-
		44 chicks	-	7	-	100	-
This study 1965	Miquelon L. Alberta	21 adults	23 adults	59	59	29	73
	Beaverhill L. Alberta	8 chicks	10 chicks	25	20	0	0

8.4 Nematodes. *Aprocta turgida* was found in the nasal and orbital cavities of adult gulls only. The total extensity of infection with *A. turgida* was greater in the Ring-billed Gulls than in the California Gulls. An average of two *A. turgida* were found in the infected Ring-billed Gulls.

It can be concluded, from the observations on the helminth fauna of the gulls, that the California and Ring-billed Gulls show a quantitive variation of similar helminth species, which is probably due to a quantitative difference in the intake of similar kinds of food. The obtained results lend additional support to the conclusion (section 7) that the two gull species have slightly different food niches.

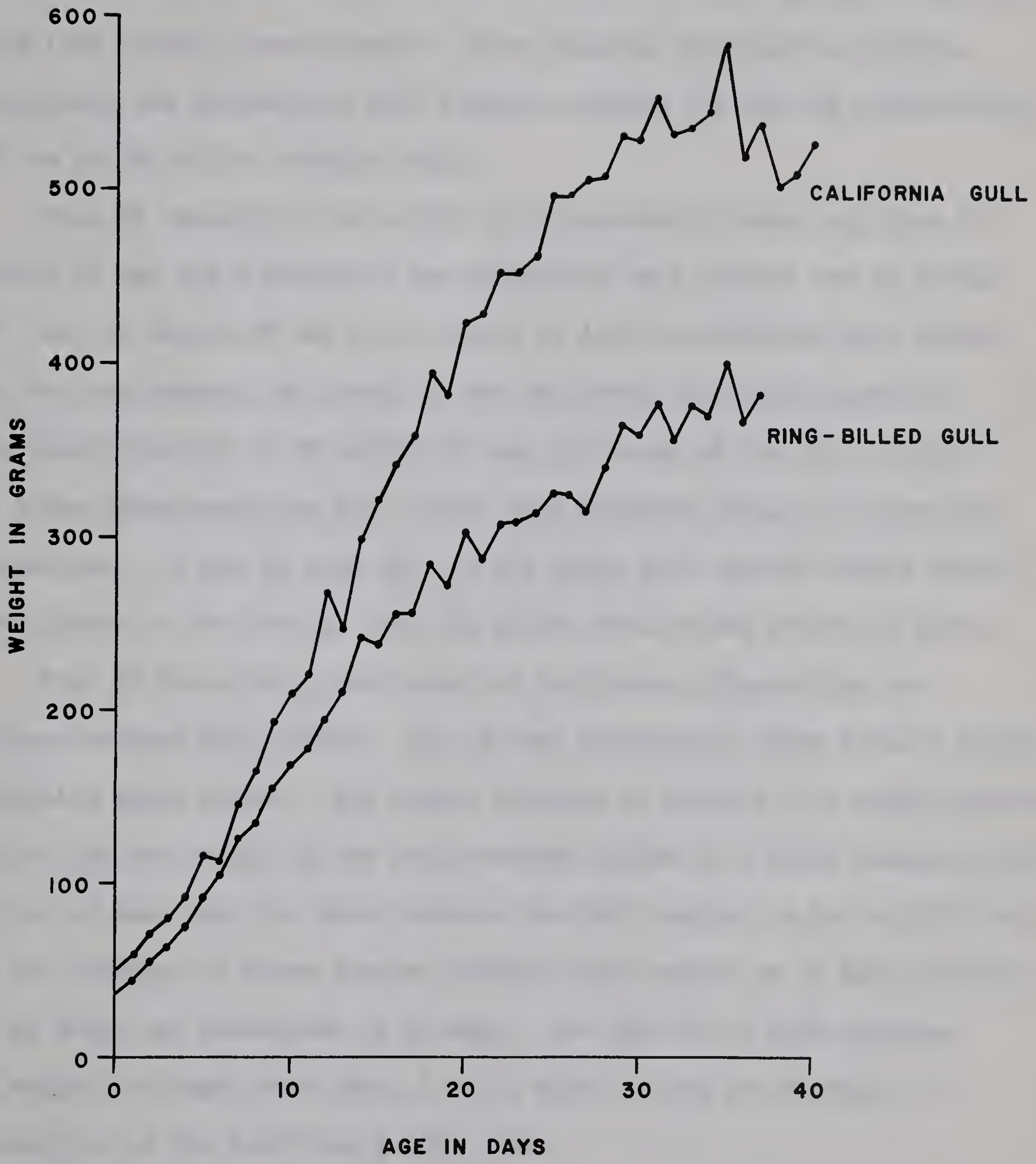
9. GROWTH

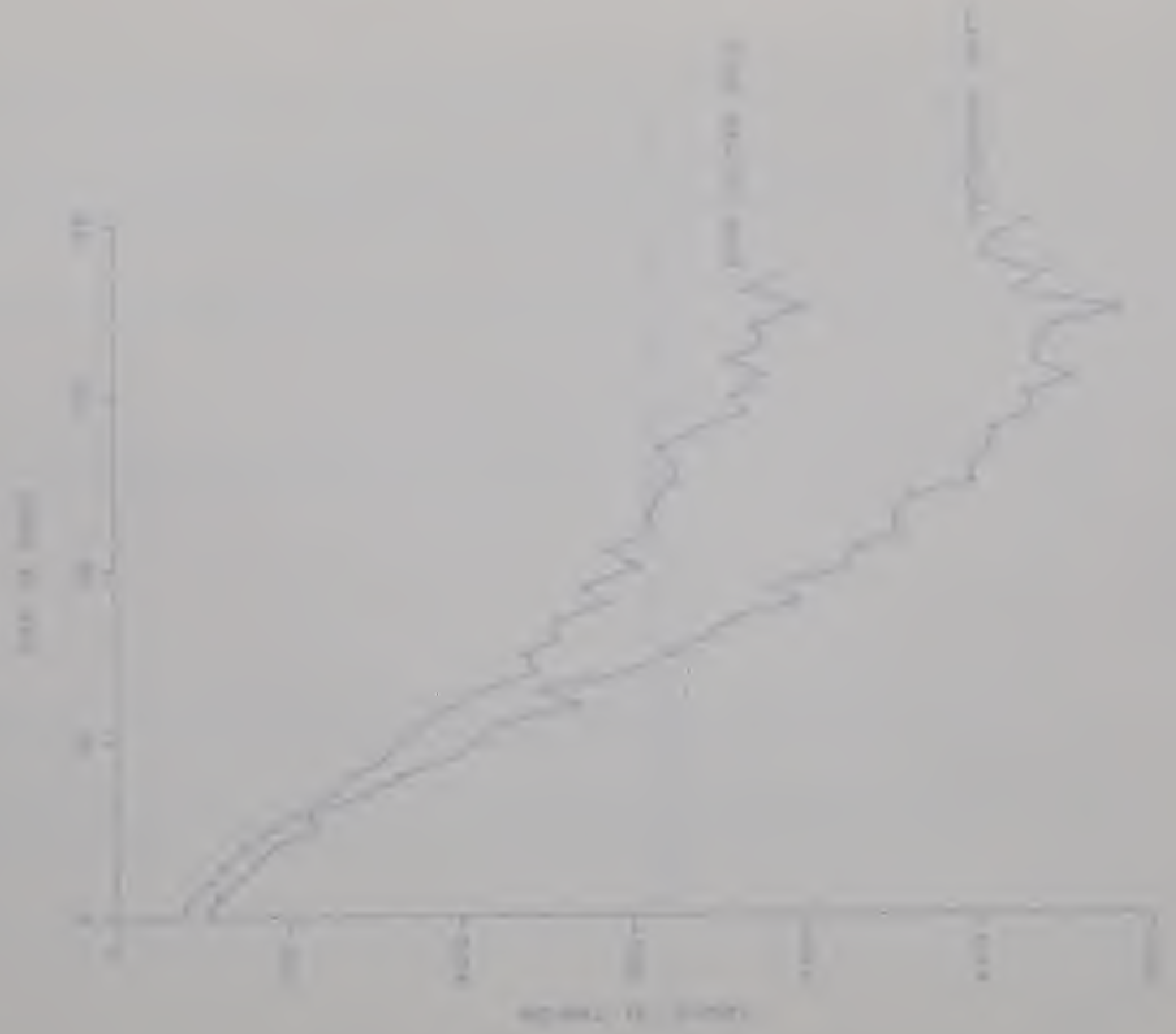
Fig. 18 and Table 33 summarize the weight records of 28 broods of the California Gull and 31 broods of the Ring-billed Gull.

Table 33. Growth of California and Ring-billed Gulls, body weight in grams

California Gull				Ring-billed Gull			
Days after hatching	Sample Size	Mean	± SE	Days after hatching	Sample Size	Mean	± SE
0	24	50.9	± 0.8	0	39	38.5	± 0.7
1	26	59.5	1.2	1	34	45.5	0.9
2	17	70.8	1.6	2	37	55.6	1.1
3	23	79.9	3.1	3	37	65.1	1.1
4	18	92.2	2.3	4	29	76.9	1.4
5	13	114.9	6.2	5	27	91.8	2.3
6	16	111.4	3.5	6	21	106.3	2.5
7	12	145.4	8.6	7	23	125.6	4.1
8	14	164.8	9.2	8	23	135.5	4.7
9	12	192.8	12.5	9	19	156.1	5.9
10	14	209.7	7.8	10	22	168.9	5.6
11	9	219.8	10.7	11	13	176.4	5.0
12	12	268.6	9.7	12	19	196.1	5.9
13	11	247.4	16.1	13	14	212.2	8.7
14	16	299.9	15.5	14	20	241.3	9.5
15	14	320.4	16.3	15	18	238.9	10.0
16	14	340.8	17.1	16	20	254.2	9.6
17	18	357.8	16.1	17	20	253.6	10.3
18	11	395.5	19.7	18	18	284.5	10.5
19	17	381.4	17.0	19	22	272.8	8.5
20	12	422.4	20.1	20	19	302.1	11.4
21	15	428.5	18.6	21	20	287.3	10.9
22	13	452.4	26.2	22	20	307.1	13.5
23	19	451.2	14.6	23	20	308.2	12.3
24	10	460.4	30.5	24	12	311.5	17.1
25	15	498.5	22.2	25	18	325.8	11.0
26	16	496.8	19.8	26	20	322.2	12.4
27	14	505.4	26.4	27	18	316.3	14.2
28	14	508.4	25.0	28	19	340.0	13.9
29	14	531.4	25.2	29	21	365.2	12.8
30	21	528.2	18.3	30	20	359.5	10.1
31	10	554.5	35.7	31	20	377.2	16.4
32	15	531.8	19.1	32	20	358.3	12.4
33	9	536.7	28.3	33	18	374.2	14.5
34	13	546.4	26.2	34	16	370.1	12.5
35	8	585.6	34.3	35	13	400.5	18.3
36	13	520.6	27.2	36	11	365.2	11.9
37	4	539.9		37	14	382.3	19.0
38	8	501.3					
39	2	508.7					
40	6	527.4					

Fig. 18. Growth of California and Ring-billed Gull chicks in 1964


600
500
400
300
200
100
0
WEIGHT IN GRAMS
0
10
20
30
40
AGE IN DAYS
CALIFORNIA GULL
RING-BILLED GULL

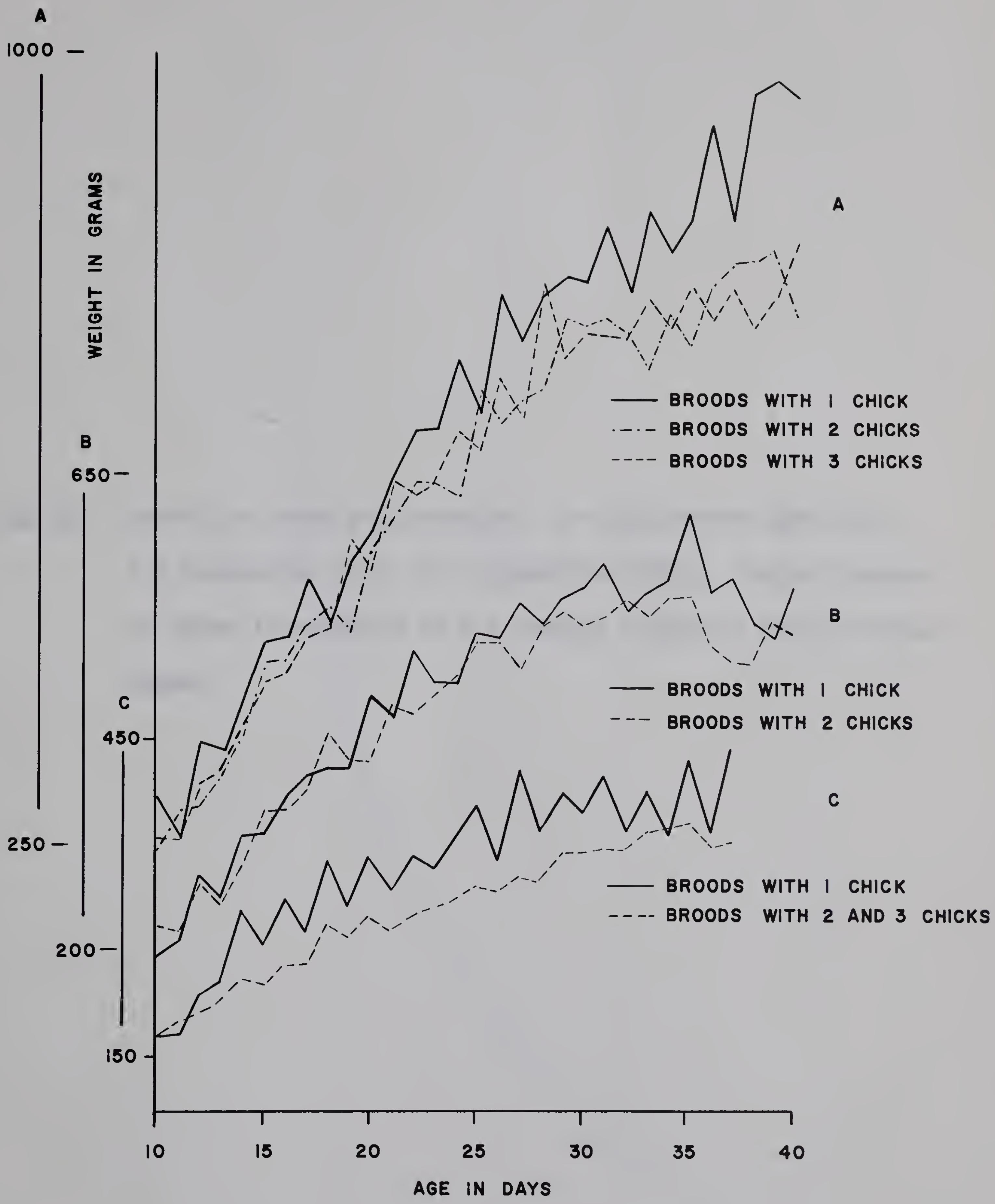


The average weights at fledging for 18 California and 30 Ring-billed Gull juveniles were 573g (435 to 675) and 377g (260 to 503), respectively. The average weights of 39 adult California and 39 adult Ring-billed Gulls which were collected during the breeding season were 771g (610 to 964) and 497g (390 to 670), respectively. These figures show that the average California and Ring-billed Gull juvenile reaches 74% and 76% respectively, of the weight of the average adult.

Fig. 19 summarizes the weight of chicks, over 10 days old, from 20 broods of one and 8 broods of two California Gull chicks; and 18 broods of one, 10 broods of two and 3 broods of three Ring-billed Gull chicks. In the last species the broods of two and three are lumped together. The weight records of 29 broods of one, 25 broods of two and 11 broods of three Glaucous-winged Gull chicks from Mandarte Island are shown for comparison. It can be seen that in all three gull species single chicks grew faster on the average than did chicks from broods of two or three.

Fig. 20 shows the growth rates of California, Ring-billed and Glaucous-winged Gull chicks. Fig. 20 was constructed after Drent's (1965) composite graph method. The weight increase is plotted on a semi-logarithmic scale with the weight of the newly-hatched chicks as a fixed starting point. It can be seen that the three species are very similar up to the 20th day. On the average all three species doubled their weight by 4½ days, trebled by 10 days, and quadrupled by 20 days. The time for a 100% increase in weight is longer each time, i.e., 4 days, 6 days and 10 days, an indication of the declining growth rate.

Fig. 19 Growth in broods of one, two and three chicks of Glaucous-winged, California and Ring-billed Gulls. A - Glaucous-winged Gull, B - California Gull, C - Ring-billed Gull. Mean weights given in broods of one, two and three chicks.


A
1000
B
650
C
450
250
200
150
WEIGHT IN GRAMS
10
15
20
25
30
35
40
AGE IN DAYS
A
BROODS WITH 1 CHICK
BROODS WITH 2 CHICKS
BROODS WITH 3 CHICKS
B
BROODS WITH 1 CHICK
BROODS WITH 2 CHICKS
C
BROODS WITH 1 CHICK
BROODS WITH 2 AND 3 CHICKS

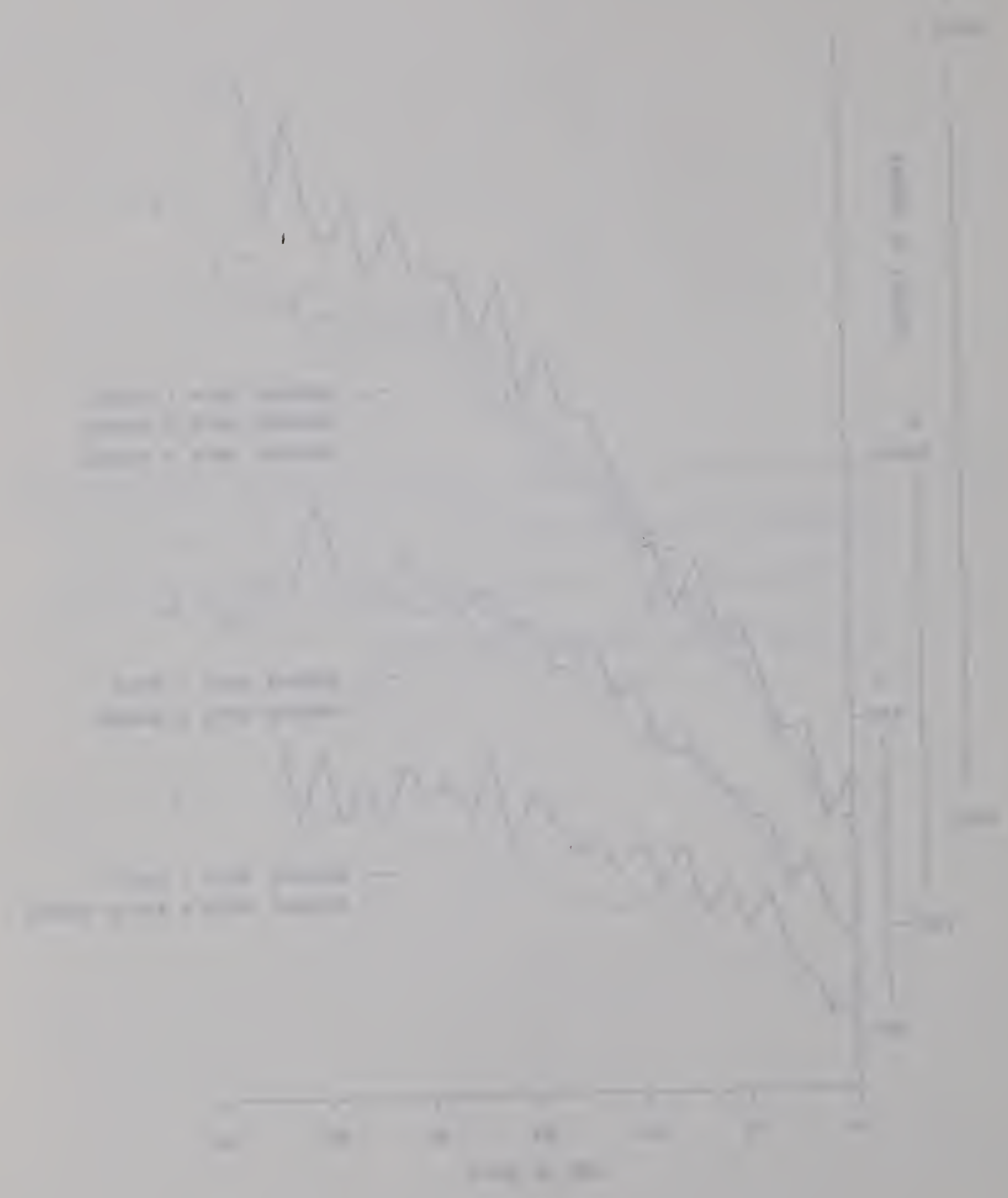
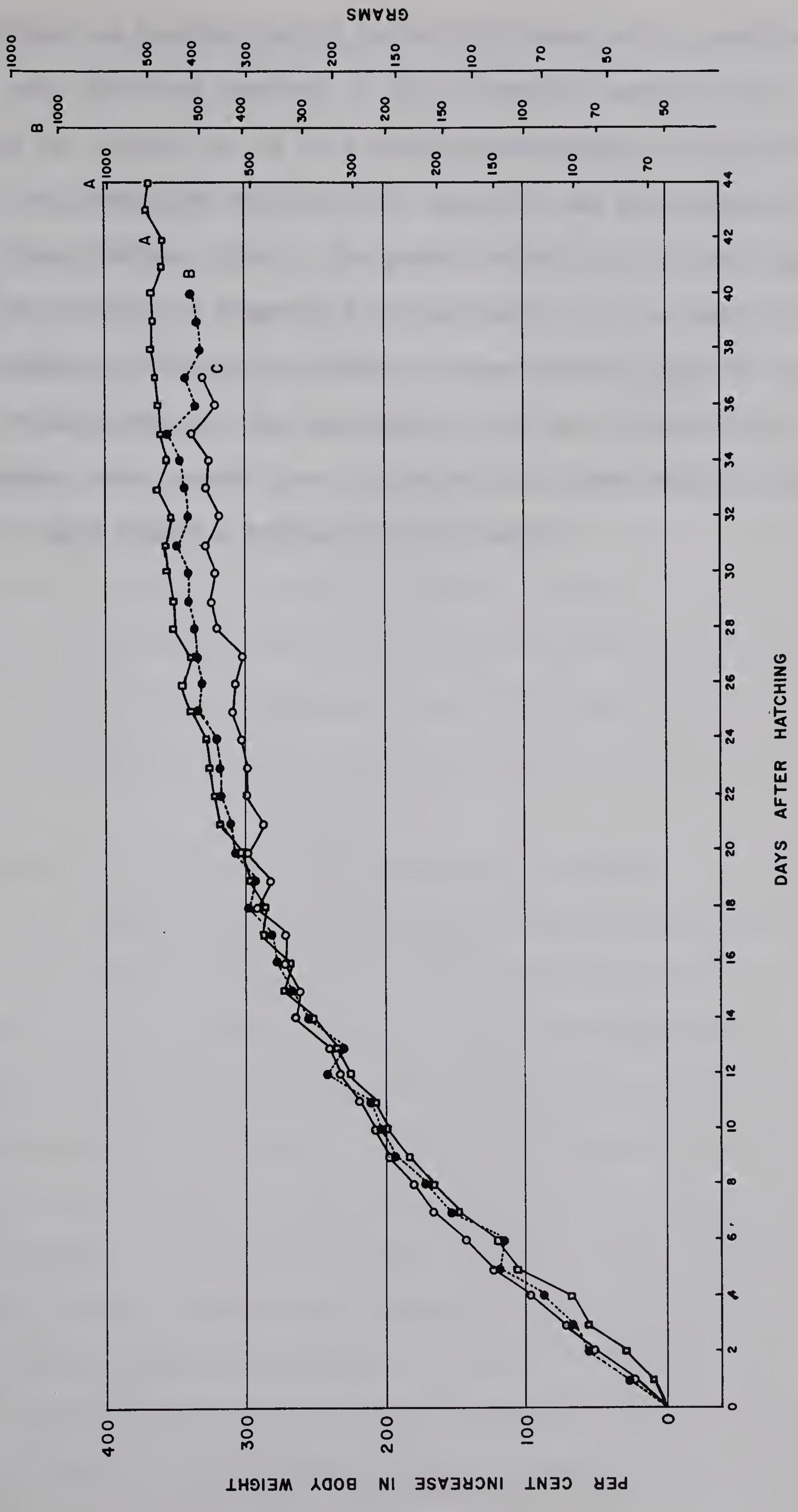


Fig. 20. Growth in three gull species. A = Glaucous-winged Gull, B = California Gull, C = Ring-billed Gull. Weight increase is shown in relation to the average weight of newly hatched chicks.


PER CENT INCREASE IN BODY WEIGHT
0
100
200
300
400
DAYS AFTER HATCHING
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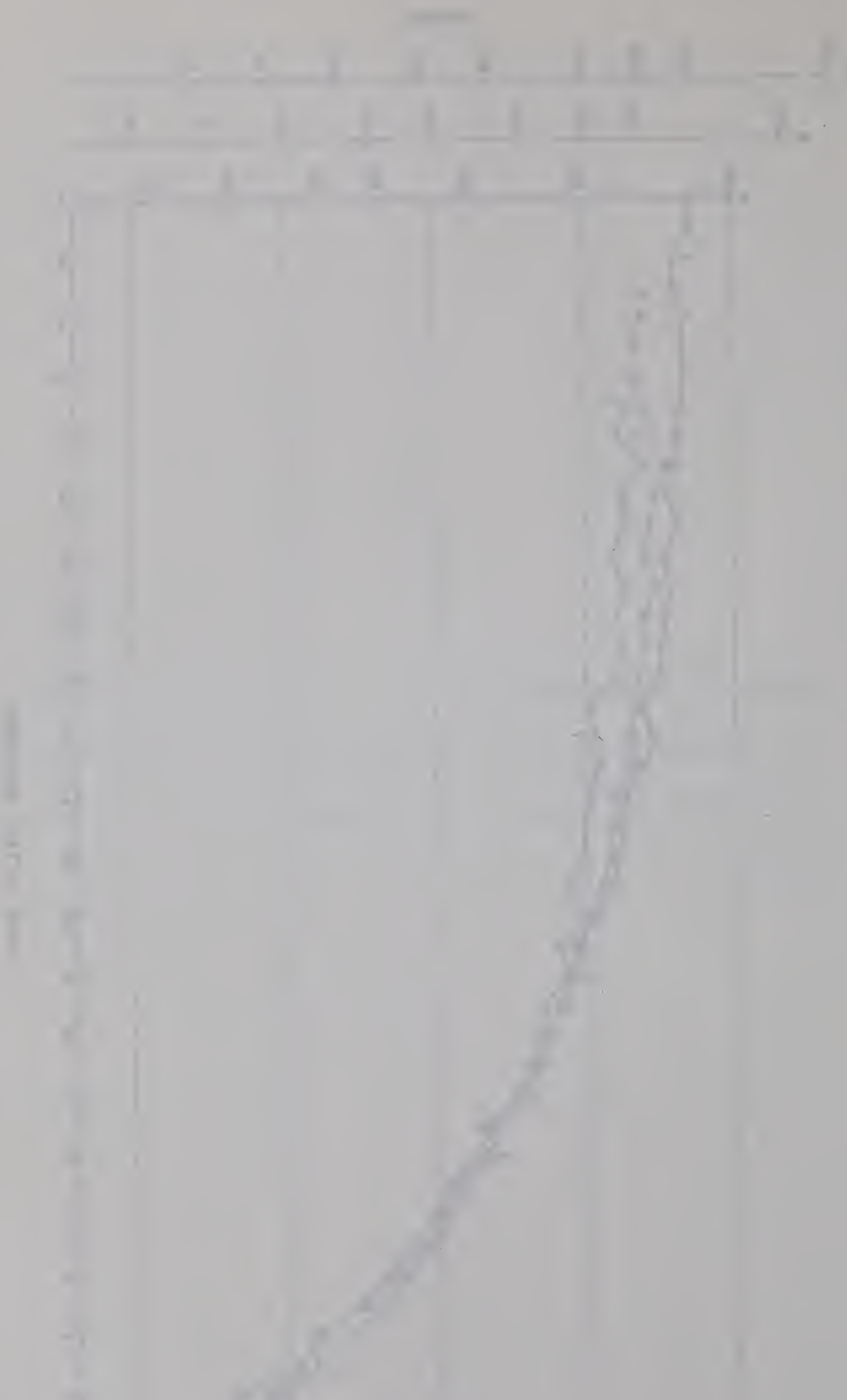

Although the breeding period in the California and Ring-billed Gulls is much shortened compared to that of coastal nesting gulls, the former two species do not show adaptive shortening of the growth period. That growth can be adaptively shortened has been shown for the family Sulidae (Nelson, 1966). The growth period of the Gannet (Sula bassana) in Scotland is compressed by comparison with the rest of the family breeding at tropical latitudes. Nelson (1966) suggested that the most advantageous way for the Gannet to use the available food is to compress chick growth into the period when there are most fish in order to give chicks a substantial fat reserve.

10. CONCLUDING DISCUSSION OF ADAPTATIONS OF GULLS TO BREEDING IN THE INLAND HABITAT

There are not many basic differences between inland breeding gull species and marine forms. Growth and reproductive rates of the California and Ring-billed Gulls appeared to be similar to those of Glaucous-winged Gulls. Although predation pressure on the gulls at Miquelon Lake was greater than on the Glaucous-winged Gulls on Mandarte Island the former still are ground-nesters like the latter. Mew Gulls nest occasionally and Bonaparte Gulls (Larus philadelphia) regularly in trees (Godfrey, 1966) in the inland habitat, presumably to counteract predation. However, the presence of many colonies of California and Ring-billed Gulls on islands in the interior of North America shows that those two species can maintain themselves well in this type of nesting habitat, which is relatively free from mammalian predation.

Apparent adaptations of the two species to breeding inland are the ability to exploit a seasonally abundant supply of insects and rodents and a short breeding season. The short breeding season is marked by a compressed pre-egg period, a short laying period and a reduction of repeat laying as compared to marine nesting gulls. Lack (1954) suggested that the time of production is governed by natural selection in such way that it takes place when the food supply for the young is optimal. It has been seen that rodents formed an important part of the diet in California and Ring-billed Gulls during the whole breeding season, while the appearance of insects in the gull diet closely coincided with the onset of hatching of the chicks at Miquelon Lake. The timing of the appearance of these two food sources on the

breeding grounds may be important in governing the breeding chronology in California and Ring-billed Gulls. It is possible that the ability to renest has been reduced in the California and Ring-billed Gulls since late clutches, in view of the limited insect supply, yield practically no chicks. Repeat laying would thus confer no advantage. Other colonial birds nesting inland such as Common Terns and Double-crested Cormorants (Phalacrocorax auritus) lay later in the season than California and Ring-billed Gulls. Common Terns at Miquelon Lake were observed to renest in July, three weeks after the first hatching occurred. Double-crested Cormorants in Manitoba can lay eggs from mid-May til mid-July (McLeod and Bondar, 1953; Munro, 1927). The ability of Common Terns and Double-crested Cormorants to renest later in the season may be related to their diet. Double-crested Cormorants eat chiefly fish (Lewis, 1929; McLeod and Bondar, 1953; Mendall, 1935) and the diet of Common Terns is composed mainly of fish and crustaceans (Mendall, 1935). These food sources may be available for a longer period of the season to these birds than insects to the California and Ring-billed Gulls. Other indications that a seasonally limited food supply may be responsible for the shortened breeding season are the earlier departure of the adults than the young from the breeding grounds and an earlier seasonal decline of fledgling production in California and Ring-billed Gulls than in the marine Glaucous-winged Gulls. If a seasonal nature of the food supply and of the most favourable period for post-fledgling survival sets the limits to the laying period, one would expect selection to act against the very late breeders.

The laying periods of the California and Ring-billed Gulls are synchronized to the extent that the large majority of clutches are

started at the beginning of the laying season and that the lengths of the laying periods are shortened as compared to those of gull species nesting along marine coasts. Kruuk (1964) and Patterson (1965) suggested that the synchronized egg-laying at the start of the laying period in the Black-headed Gulls, nesting on dunes at Ravenglass, England, had an anti-predator function. Patterson (1965) recorded the proportion of broods of Black-headed Gulls reaching the fledging stage for the different time classes and found that broods hatched during the peak of the hatching curve had a much higher success than the late broods. The higher losses of the later broods were mainly the result of predation by foxes. The synchronized clutch initiation at the start of egg-laying in the inland nesting California and Ring-billed Gulls may, besides being possible caused by a seasonal nature of the food supply, be also influenced by predation pressure as has been suggested by Kruuk (1964) and Patterson (1965) for the Black-headed Gulls.

With respect to the lengths of the laying periods, those of the gull species nesting at Miquelon Lake were approximately three weeks shorter than those of the populations of Black-headed Gulls nesting in a fresh water habitat near Oslo, Norway (Ytreberg, 1956) and on the dunes at Ravenglass, England (Patterson, 1965; Weidmann, 1956). Since all three gull species suffered extensive predation, the shorter laying periods of the California and Ring-billed Gulls than those of the Black-headed Gulls may point to the effects of a more seasonally limited food supply for the inland nesting species rather than to the effects of predation.

Although there are indications that a seasonally limited food supply favours a shortened breeding season for the California and Ring-billed Gulls, experiments are needed to test this hypothesis. This can be done by comparing growth rates between early and late hatched chicks and by adding chicks to make up broods above normal size. A slower growth rate of late hatched chicks and the inability to raise broods above normal size would point to the effects of a limiting food supply. Glaucous-winged Gulls on Mandarte Island are able to raise four, five and even six young, possibly because the present situation there is unusually favourable for the feeding of that species (Lack, 1966).

In 1964, clutches of California and Ring-billed Gulls were removed to obtain replacement clutches from which the growth rates of gull chicks could be compared with those of initial clutches. No replacements resulted, possibly because the removal date was too late. In 1965, clutches were removed at an earlier date than in the previous year and an experiment of adding chicks to make up broods above normal size was started. The results of the experiments were inconclusive because of the general high loss of eggs and chicks in that year.

Results obtained in an experiment in 1967, to test the relationship of growth and survival to the time of hatching of the chicks, seem to contradict the hypothesis that a seasonally limited food supply governs the short breeding season of the inland nesting California and Ring-billed Gulls. (Addendum)

SUMMARY

1. The juveniles of the California and Ring-billed Gulls raised at Miquelon Lake winter chiefly along the coast of California and the West Coast of Mexico.
2. The first Ring-billed Gulls arrived in the last days of March in the Edmonton region and on the nesting grounds simultaneously. The first California Gulls were observed a week later. Snow depth did not seem to influence the time of the birds' arrival. Air temperature may be important as a threshold factor in that the birds may not arrive unless a certain temperature has been surpassed. In the autumn, the Ring-billed Gulls remained in the Edmonton region for a longer time than the California Gulls.
3. In contrast to gulls breeding in coastal Europe, whose time of arrival in the spring depends on the melting of the ice, the two species at Miquelon Lake occupied the breeding grounds before snow and ice disappeared. The pre-egg periods of the California and Ring-billed Gulls were short when compared to that of the marine nesting Glaucous-winged Gulls.
4. Two daily peaks of activity by the gulls occurred during the pre-egg period on the breeding grounds. During this period the gulls did not spend the night on the islands. The gull's absence from the breeding colony at night during the pre-egg period may reduce predator facilitation.
5. The date of mean clutch commencement in 1964 was May 8 for both species, in 1965 it was May 10 for the Ring-billed Gulls, and May 11 for the California Gulls. The date of mean clutch commencement appeared to be influenced by such factors as air temperature and

disturbance. Food was not a primary factor in determining the time of reproduction of the two species.

6. The egg-laying periods of the inland breeding California Gulls and Ring-billed Gulls are much shorter than those in gull species nesting in a coastal climate. The extent of repeat-laying in the two species was much reduced compared to that in the marine nesting gulls.
7. The average dates of the commencement of hatching of the California Gulls fell on June 6 in 1964 and June 13 in 1965 and those of the Ring-billed Gulls fell on June 4 in 1964 and June 14 in 1965. The later hatching of both species in 1965 was linked to a later commencement of laying and possibly increased human and predatory disturbance in that year.
8. In California Gulls only 26% and 51% of the full incubation effectiveness was achieved after the first and second egg were laid, respectively. The corresponding figures for the Ring-billed Gulls were 28% and 54%. The effectiveness of incubation during laying in the California and Ring-billed Gulls was similar to that of gulls nesting in a marine habitat.
9. The average incubation periods of the California and Ring-billed Gulls were 26.6 ± 0.09 and 25.0 ± 0.10 days, respectively. No adaptive shortening of these periods was apparent when they were compared with those of coastal nesting gull species.
10. The California and Ring-billed Gulls fledged at the average age of 40 and 37.2 days, respectively. Considering their weights, the fledging period of these species is similar to that of the marine Glaucous-winged Gulls and Herring Gulls. California and Ring-billed Gulls remained on the breeding grounds on the average of 11 days

after fledging, which is a period similar to that in the Glaucous-winged Gulls.

11. Most families of California and Ring-billed Gulls appear to break up at the colony as the counts show that the parents slightly preceded the juveniles in departure. The earlier departure of the adults than the juveniles may indicate that the food supply at the end of July was limited in the vicinity of the breeding grounds. Once the juveniles leave the islands, they do not appear to return to Miquelon Lake.

12. The average clutch sizes of the California Gulls were 2.82 ± 0.03 in 1964 and 2.73 ± 0.04 in 1965. The corresponding figures for the Ring-billed Gulls were 2.92 ± 0.02 in 1964 and 2.85 ± 0.02 in 1965. The clutch sizes of the California and Ring-billed Gulls were similar to those of coastal breeding gulls.

13. The total egg losses for the California Gulls were similar in 1964 and 1965, but for the Ring-billed Gulls it increased significantly in 1965. The egg losses for the California Gulls in both years and the Ring-billed Gulls in 1964 were similar to those for gull studies in marine habitats.

14. Most of the egg losses of both species occurred in the categories "infertility or embryonic death" and "disappeared and presumed eaten". The greatest loss of eggs of the Ring-billed Gulls in 1965 occurred in early layers of this species and was either the result of infertility or the cessation of development at an early embryonic stage. The extensive egg loss of the Ring-billed Gulls in 1965 may have been caused by a combination of bad weather and visits of nocturnal predators.

15. Eggs were also lost as a result of parents being killed by a nocturnal predator. Feathers from the areas where the decapitated bodies of the adult gulls were found matched those of the Great Horned Owl. No adults were found dead as a result of predation after the eggs hatched. No predation was observed on adults of the coastal Glaucous-winged Gulls nesting on Mandarte Island.

16 The majority of the California and Ring-billed Gull eggs, like those of the Glaucous-winged Gulls, disappeared or were eaten during laying and the first week of incubation. One of the roles of incubation behaviour besides providing the warmth necessary for the development of the gull embryo, appears to be reduction of egg predation.

17. In 1964 each species raised on the average, one juvenile per nest, which demonstrates that they can produce offspring successfully when nesting together. No chicks of either species fledged at Miquelon Lake in 1965. This was only a local phenomenon, since the fledging success of California and Ring-billed Gulls 22 miles away appeared normal.

18. In the majority of cases, the cause of chick death could not be ascertained because the chicks disappeared between my visits. The greatest known cause of chick mortality was predation. The California Gulls in both years and a Great Horned Owl (?) in 1965 were the greatest predators on gull chicks.

19. The decline of the number of chicks which fledged from late clutches in the California and Ring-billed Gulls came much earlier than for the Glaucous-winged Gulls.

20. Weekly mortality rates of chicks were similar in California, Ring-billed and Glaucous-winged Gulls. As in the Glaucous-winged Gulls, the greatest chick mortality in the gull species at Miquelon Lake occurred in the first week of life.
21. The reproductive success of the California and Ring-billed Gulls in 1964 was similar to that of the average over a five-year period in the Glaucous-winged Gulls. No single factor can be held responsible for the poor reproduction success of California and Ring-billed Gulls in 1965. Parental neglect describes the state of affairs without explaining it.
22. California and Ring-billed Gulls avoid areas with dense vegetative cover at the time of territorial establishment, which is thought to be an anti-predator mechanism.
23. Clutches of California Gulls on a peninsula at Miquelon Lake were all destroyed by coyote predation. The nesting of gulls on islands is thought to be an adaptation to counteract mammalian predation.
24. California Gulls nested along the peripheries of both islands and on the most elevated boulder-strewn area on island A. The Ring-billed Gulls nested farther from the water and in relatively flatter areas. Both species could nest in the same habitat. The interspecific differences in the choice of nest-site between the two species as compared to intraspecific variation in nesting habitat of other gull species did not appear to be very significant.
25. The nests of the California Gulls were randomly distributed, those of the Ring-billed Gulls showed a significant deviation from randomness in the direction of aggregated spacing, while that of the Glaucous-winged Gulls showed a significant deviation from

randomness in the direction of uniform spacing. The aggregated nesting pattern of the Ring-billed Gulls may be an anti-predator mechanism. This aggregated nesting pattern does not appear to be a special adaptation to inland conditions.

26. The main diet of the Ring-billed Gulls at Miquelon Lake changed from grain in May, to insects in June and organic refuse in July. No food group dominated for the California Gull in May, but as in the Ring-billed Gull the diet changed from insects in June to refuse in July. The diet of the chicks of both species was similar to that of the adults in June and July. When _Microtus pennsylvanicus_ became extremely abundant in the spring of 1966, more than 90% of the pellets of both gull species contained this rodent, showing the opportunistic feeding habits of the gulls.

27. It appears that the California and Ring-billed Gulls have slightly different food niches. Both species feed on grain, insects, rodents, birds and bird eggs, but in the Ring-billed Gull diet there is more grain, more mice, fewer birds and waterfowl eggs. The California Gull's diet consists of more amphibians, waterfowl eggs, young waterfowl and larger rodents.

28. The helminth fauna of the California and Ring-billed Gulls at Miquelon Lake show a quantitative variation of similar helminth species. This is probably due to a difference in quantitative intake of generally similar food.

29. The extensity of the occurrence of _Plagiorchis elegans_, _Diplostomum spathaceum_, _Hymenolepis californicus_ and _Aprocta turgida_ and the intensity of _Plagiorchis elegans_ and _Paricterotaenia porosa_ were

significantly greater in the Ring-billed Gull than in the California Gull.

30. The greater occurrence of Diphyllobothrium dendriticum, Schistocephalus sclidus, Diplostomum spathaceum and Cotylurus erraticus in the Ring-billed Gull indicates that this bird eats more infected fish than does the California Gull.

31. Although the breeding seasons of California and Ring-billed Gulls are much shortened compared to that of the coastal Glaucous-winged Gulls, the two former species do not show an adaptive shortening of the growth period. The California and Ring-billed Gulls as well as the Glaucous-winged Gulls doubled their weight by 4½ days, trebled by 10 days, and quadrupled by 20 days. The California and Ring-billed chicks at the time of fledging reached 74% and 76% respectively, of the weight of the average adult. In all species, single chicks grew faster than those in broods of two or three.

32. There are few basic differences between inland breeding gull species and marine forms. The apparent adaptation to breeding in an inland habitat is a shortened breeding season, marked by a compressed pre-egg period, a short laying period, and a reduction of repeat laying as compared to marine nesting gulls. The function of this adaptation appears to be to achieve a maximum reproductive output of young by making the most use of a seasonally limited food supply.

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION, 1957
The A.O.U. checklist of North American Birds. A.O.U., 1957, Baltimore.

ANDERSON, W. 1965.
Waterfowl production in the vicinity of gull colonies. Cal. Fish and Game, 5: 5-15.

AUSTIN, O.L. 1946.
The status of the Cape Cod terns in 1944, a behaviour study. Bird Banding, 17: 10-27.

BARTH, E.K. 1967
Standard body measurements in Larus argentatus, L. fuscus, L. canus, and L. marinus. Nytt Mag. Zool., 14: 7-83.

__________ 1955.
Egg-laying, incubation and hatching of the Common Gull (Larus canus). Ibis, 97: 222-239.

BARTHOLOMEW, G.A. 1942.
The fishing activities of Double-crested Cormorants in San Francisco Bay. Condor, 44: 13-21.

BEHLE, W.H. 1958.
The bird life of Great Salt Lake. University of Utah Press, 203 pp.

BEHLE, W.H. AND W.A. GOATES, 1957.
Breeding biology of the California Gull. Condor, 59: 235-246.

BELOPOLSKII, L.O. 1957.
Ecology of sea colony birds of the Barents Sea. Israel program for scientific translations, Jerusalem, 1961. 449 pp.

BENT, A.C. 1921.
Life histories of North American gulls and terns. U.S. Nat. Mus. Bull. 113. 337 pp.

BERGMAN, G. 1939.
Untersuchungen über die Nistvogel fauna in einem Schärengebiet westlich von Helsingfors. Acta Zool. Fenn., 23: 1-134.

BROWN, W.C. 1950.
Cestode parasites of the California Gull (Larus californicus) in the Great Salt Lake area. Unpublished Master's Thesis, University of Utah. 37 pp.

CHURA, N.J. 1962.
Behaviour of the California Gull feeding on a large Mallard duckling. Auk, 79: 484-485.

CLARK, P.J. and F.C. EVANS, 1954.
Distance to nearest neighbour as a measure of spatial relationships in populations. Ecology, 35: 445-453.

COTTAM, C. 1945.
California Gulls feeding on midges. Condor, 47: 216.

COULSON, J.C. and E. WHITE. 1961.
An analysis of factors influencing the clutch size of the Kittiwake. Proc. Zool. Soc. London, 139: 207-217.

—————, 1960.
The effect of age and density of breeding birds on the time of breeding of the Kittiwake, Rissa tridactyla. Ibis, 102: 71-86.

—————, 1959.
The post-fledging mortality of the Kittiwake. Bird study, 6: 97-102.

—————, 1956.
A study of colonies of the Kittiwake Rissa tridactyla. Ibis, 98: 63-79.

DRENT, R.H. 1965.
Breeding biology of the Pigeon Guillemot, Cepphus columba. Ardea, 53: 99-160.

DRENT, R.H., G.F. van TETS, F. TOMPA and K. VERMEER. 1964.
The breeding birds of Mandarte Island, British Columbia, Can. Field Nat., 78: 208-263.

DROST, R., E. FOCKE, G. FREYTAG. 1961.
Entwicklung und Aufbau einer Population der Silbermöwe, Larus argentatus argentatus. J.f. Orn. 102: 404-429.

EMLEN, J.T. 1956.
Juvenile mortality in a Ring-billed Gull colony. Wilson Bull., 68: 232-238.

EMLEN, J.T., D.E. MILLER, R.M. EVANS and D.H. THOMPSON. 1966.
Predator-induced parental neglect in a Ring-billed Gull colony. Auk, 83: 667-679.

ERRINGTON, P.L., F. HAMERSTROM and F.N. HAMERSTROM. 1940.
The Great Horned Owl and Its Prey in North-Central United States. Research Bull., 277: 759-850.

FARLEY, F.L. 1932.
Birds of the Battle River Region. Inst. App. Art. Ltd., Edmonton. 85 pp.

FARNER, D.S. 1964.
The photoperiodic control of reproductive cycles in birds. Amer. Sci. 52: 137-156.

FISHER, J. and R.M. LOCKLEY, 1954.
Sea-birds. Collins, London. 320 pp.

FORDHAM, R.A. 1964.
Breeding biology of the Southern Black-backed Gull. II: Incubation and the Chick Stage. Notornis, 11: 110-126.

GODFREY, W.E. 1966.
The birds of Canada. Bull. 203. Biol. Ser. 73. Nat. Mus. of Can. 428 pp.

GOETHE, F. 1960.
Felsbrutertum und weitere beachtenswerte Tendenzen bei der Silbermöwe. Proc. XII Int. Orn. Congr: 252-258.

_________, 1956.
Die Silbermöwe. Die Neue Brehm - Bücherei No. 182. Wittenberg. 95 pp.

_________, 1955.
Beobachtungen bei der Aufzucht junger Silbermöwen. Zeitschr. Tierpsych., 12: 402-433.

_________, 1953.
Experimentelle Brutbeendigung und andere brutethologische Beobachtungen bei der Silbermöwe (Larus a. argentatus P.)J.f.Orn., 94: 160-174.

_________, 1937.
Beobachtungen und untersuchungen zur Biologie der Silbermöwe (Larus a. argentatus P.) auf der Vogel-insel Memmertsand. J. f. Orn., 85: 1-119.

GREENHALGH, C.M. 1952.
Food habits of the California Gull in Utah. Condor, 54: 302-308.

HANSON, W.C. 1963.
Census of Ring-billed and California Gull colonies in Eastern Washington. Condor, 65: 163-164.

HARRIS, M.P. 1965.
The food of some Larus gulls. Ibis, 107: 43-53.

_________, 1964.
Aspects of the breeding biology of the gulls Larus argentatus, L. fuscus and L. marinus. Ibis, 106: 432-456.

HOUSTON, C.S. 1963.
R.F. Oldaker, the man who reads gull bands with a telescope. Blue Jay, 21: 53-57.

ISHUNIN, G.I. 1964.
The nutrition of the Black-headed Gull in the area of Lake Sivash (in Russian). Ornitologya, Moscow, 6: 471-472. Ref. ZH. Biol., 1964, No. 161209.

JOHNSTON, D.W. and M.E. FOSTER. 1954.
Interspecific relations of breeding gulls at Honey Lake, California. Condor, 56: 38-42.

KAHL, M.P. 1964.
Food ecology of the Wood Stork (Mycteria americana) in Florida, Ecol. Mon., 34: 97-117.

KEITH, J.A. 1966.
Reproduction in a population of Herring Gulls (Larus argentatus) contaminated by DDT. J. Appl. Ecol. (Suppl.), 3: 57-70.

KEREKES, J. 1965.
A comparative limnological study of five lakes in central Alberta. Unpublished Master's Thesis, University of Alberta, 164 pp.

KIRKMAN, F.B. 1937.
Bird behaviour. Nelson, London.

KRUUK, H. 1964.
Predators and anti-predator behaviour of the Black-headed Gull (L. ridibundus). Behaviour Suppl., 11: 1-130

LACK, D. 1966.
Populations studies of birds. Clarendon Press. Oxford. 341 pp.

————, 1954.
The natural regulation of animal numbers. Oxford Univ. Press. 343 pp.

LEWIS, H.F. 1941.
Ring-billed Gulls of the Atlantic coast. Wilson Bull., 53: 22-30.

————, 1929.
The natural history of the Double-crested Cormorant. Ph.D. Thesis Cornell University, Ithaca. New York. 94 pp.

LOCKIE, J.D. and D.A. RATCLIFFE. 1964.
Insecticides and Scottish Golden Eagles. Brit. Birds, 57: 89-102.

McLEOD, J.A. and BONDAR, G.F. 1953.
A brief study of the Double-crested Cormorant on Lake Winnipegosis. Can. Field Nat., 67: 1-11.

MacMULLAN, R.A. and L.L. EBERHARDT. 1953.
Tolerance of incubating pheasant eggs to exposure. J. Wildl. Mgmt., 17: 322-330.

MENDALL, L.M. 1935.
The relationship of certain sea-birds to the fishing industry of the State of Maine. Bull. Dept. Sea and Shore Fish. Maine 27 pp.

MEYERRIECKS, A.J. 1965.
Ring-billed Gulls gorge on Fiddler Crabs. Wilson Bull., 77: 402-403.

MINORANSKII, V.A. 1963.
Nesting of the Herring Gull (L. argentatus) in Lake Manych-Gudilo. N.D.V.S. Biol. Nauki, 3: 51-53.

MORENG, R.E. and R.L. BRYANT. 1956.
The resistance of the chicken embryo to low temperature exposure. Poultry Sci., 35: 753-757.

MOSS, E.H. 1959.
Flora of Alberta. Univ. of Toronto Press. 546 pp.

MOYNIHAN, M. 1962.
Hostile and sexual behaviour patterns of South American and Pacific Laridae. Behaviour, suppl. 8. 365 pp.

________, 1956.
California Gulls and Herring Gulls breeding in the same colony. Auk, 73: 453-454.

________, 1955.
Some aspects of reproductive behaviour in the Black-headed Gull. (*Larus ridibundus ridibundus* L.) and related species. Behaviour, Suppl. 4. 201 pp.

MUNRO, J.A. 1936.
A study of the Ring-billed Gull in Alberta. Wilson Bull., 48: 169-180.

________, 1927.
Observations on the Double-crested Cormorant (*Phalacrocorax auritus*) on Lake Manitoba. Can. Field. Nat., 43: 99-103.

MURIE, A. 1940.
Ecology of the coyote in the Yellowstone. U.S. Dept. Int., Natl. Park Service Fauna. Ser. 4. 206 pp.

NELSON, J.B. 1966.
The breeding biology of the Gannet *Sula bassana* on the Bass Rock, Scotland. Ibis, 108: 584-626.

NORRIS-ELYE, L.T.S. 1945.
Symbiotic tendencies among birds. Can. Field Nat., 59: 174.

ODIN, C.R. 1957.
California Gull predation on waterfowl. Auk, 74: 185-202.

PALUDAN, K. 1951.
Contributions to the breeding biology of *Larus argentatus* and *Larus fuscus* Vidensk, Medd. Dansk. Naturh. Foren., 114: 1-128.

PATTERSON, I.J. 1965.
Timing and spacing of broods in the Black-headed Gull. Ibis, 107: 433-459.

PAYNTER, R.A. 1949.
Clutch-size and the egg and chick mortality of Kent Island Herring Gulls. Ecology, 30: 146-166.

________, 1947.
The fate of Kent Island Herring Gulls. Bird Banding, 18: 156-170.

PIMLOTT, D.H. 1952.
The economic status of the Herring Gulls of the Grand Manan Archipelago, New Brunswick, 1949. Wildl. Mgmt. Bull. No. 5.76 pp.

RECHER, H.F. 1966.
Some aspects of the ecology of migrant shore birds. Ecology, 47: 393-407.

ROTHWEILER, R.A. 1960.
Food habits, movements, and nesting of gulls, Freezout Lake, Teaton County, Montana. Project No. MS844, Paper No. 494. Montana Fish and Game Dept., 26 pp. (mimeo).

SERVENTY, D.L. 1960.
Geographical distribution of living birds. In Marshall, A.J. Biology and comparative physiology of birds. Vol. I. Academic Press, New York.

SMITH, N.G. 1966.
Adaptations to cliff-nesting in some Arctic Gulls (Larus.) Ibis, 108: 68-83.

STICKELL, L.F., W.H. STICKELL and R. CHRISTENSEN. 1966.
Residues of DDT in brains and bodies of birds that died on dosage and in survivors. Science, 151: 1549-1551.

STYCZYŃSKA - JUREWICZ, E. 1962.
The life cycle of Plagiorchis elegans and the revision of the genus Plagiorchis. Act. Parasit. Pol., 10: 419-445.

TINBERGEN, N. 1959.
Comparative studies of the behaviour of gulls (Laridae): A progress report. Behaviour, 15: 1-70.

__________, 1953.
The Herring Gull's world. Collins New Nat. London. 255 pp.

TINBERGEN, N. G.J. BROEKHUYSEN, F. FEEKES, J.C. HOUGHTON, H. KRUUK and E. SZULC. 1962.
Egg-shell removal by the Black-headed Gull, Larus ridibundus; a behaviour component of camouflage. Behaviour, 19: 1-70.

VERMEER, K. 1963.
The breeding ecology of the Glaucous-winged Gull (Larus glaucescens) on Mandarte Island, B.C. Occ. Pap. B.C. Prov. Mus. 13. 104 pp.

WALES, J.H. 1926.
A note on the feeding habits of gulls. Condor, 28: 97.

WEIDMANN, U. 1956.
Observations and experiments on egg-laying in the Black-headed Gull. (Larus ridibundus L.) Brit. J. Anim. Behaviour, 4: 150-161.

WILLIAMS, C.S. and W. MARSHALL, 1938.
Duck nesting studies, Bear River Migratory Bird Refuge, Utah, 1937. J. Wildl. Mgmt., 2: 29-48.

WINGFIELD, B.H. 1951.
A waterfowl productivity study in Knudson Marsh, Salt Lake Valley, Utah. Unpublished Master's Thesis. Utah State University, Logan. 117 pp.

WOLFORD, J.W. 1966.
An ecological study of the Black-crowned Night Heron in southern Alberta. Unpublished Master's Thesis, University of Alberta, 60 pp.

WOLFSON, A. 1960.
Regulation of annual periodicity in the migration and reproduction of birds. Symp. Quant. Biol., 25: 507-514.

WUNDER, J. 1949.
The pressure of California Gull predation on waterfowl production on Utah marshes. Utah Coop. Wildl. Res. Unit Quarterly, 34-36.

YAMAGUTI, S. 1958.
Systema Helminthum I. "The digenetic trematodes of the vertebrates." Interscience publishers, London.

YOUNG, R.T. 1950.
Cestodes of California Gulls. J. Parasit., 36: 9-12.

YOUNG, S. P. 1951.
The clever coyote. I. Its history, life habits, economic status, and control. The Stackpole Co. and Wildl. Manage. Inst. Washington, D.C., 223 pp.

YTREBERG, N.J. 1960.
Some observations on egg-laying in the Black-headed Gull (*Larus ridibundus L.*) and the Common Gull (*Larus canus L.*) Nytt Mag. Zool., 9: 5-15.

——————, 1956.
Contribution to the breeding biology of the Black-headed Gull (*L. ridibundus*) in Norway. Nytt Mag. Zool. 4: 5-106.

APPENDIX 1.

Distribution in length and width of California and Ring-billed Gull eggs at Miquelon Lake in 1965.

	No. of eggs	
Length in mm.	California Gull	Ring-billed Gull
71.9-70.0	6	
69.9-68.0	26	
67.9-66.0	51	
65.9-64.0	101	6
63.9-62.0	82	21
61.9-60.0	31	44
59.9-58.0	8	82
57.9-56.0	1	65
55.9-54.0		26
53.9-52.0		7
51.9-50.0		1
Total	306	252
Mean ± SE	64.60 ± 0.13	58.53 ± 0.16

	No. of eggs	
Width in mm.	California Gull	Ring-billed Gull
49.9-48.0	39	
47.9-46.0	150	
45.9-44.0	99	10
43.9-42.0	16	110
41.9-40.0	2	113
39.9-38.0		18
37.9-36.0		1
Total	306	252
Mean ± SE	46.23 ± 0.09	41.78 ± 0.09

APPENDIX 2.

Calculation of the random distribution of inter-nest distances.

The formula: $n\left(\text{exp.}\left[(-\pi n/A)\quad(x - \tfrac{1}{2}a)^2\right] \quad - \quad \text{exp.}\left[(-\pi n/A\ (x + \tfrac{1}{2}a)^2\right]\right)$ for the calculation of the random distribution of inter-nest distances was acquired from Dr. J. M. Cullen (by correspondence). The letters in the formula denote:

A = Area with nests, which was 30,000 square feet for each of the three gull species.

n = Number of nests in the area A, which was for the Glaucous-winged Gulls, California Gulls and Ring-billed Gulls, 193, 202 and 220 nests respectively.

a = Unit of measurement used for measuring distances between nests. The unit of measurement used was one foot for each of the three gull species.

x = Distance to nearest neighbouring nest.

Example:

Assignment: To calculate the number of California Gull nests which would be 10 feet from the nearest neighbouring nest, if randomly distributed.

Solution:

$$N(x) = n\left(\text{exp.}\left[(-\pi n/A)\quad(x - \tfrac{1}{2}a)^2\right] - \text{exp.}\left[(-\pi n/A)\ (x + \tfrac{1}{2}a)^2\right]\right)$$

$$N(10) = 202\left(\text{exp.}\left[(-\pi 202/30000)\ (10 - \tfrac{1}{2}.1)^2\right] - \text{exp.}\left[(-\pi 202/30000)(10 + \tfrac{1}{2}.1)^2\right]\right)$$

$$N(10) = 202\ (\text{antilog}^{-1.8952} - \text{antilog}^{-2.3153})$$

$$N(10) = 202\ (0.150 - 0.099)$$

$$N(10) = 10.4 \text{ nests.}$$

APPENDIX 3

Adult body weights and culmen lengths of California and Ring-billed Gulls

Body weights in grams	No. of cases				Culmen length in mm.	No. of cases			
	California Gull		Ring-billed Gull			California Gull		Ring-billed Gull	
	male	female	male	female		male	female	male	female
999 - 900	3				57.9-56.0	6			
899 - 800	16	2			55.9-54.0	3			
799 - 700	4	4			53.9-52.0	5			
699 - 600		10	2		51.9-50.0	1	3		
599 - 500			13	4	49.9-48.0		4		
499 - 400			4	15	47.9-46.0		3	4	
399 - 300				1	45.9-44.0			6	
					43.9-42.0			4	1
					41.9-40.0			1	3
					39.9-38.0				3
					37.9-36.0				4
Total	23	16	19	20		15	10	15	11
Mean ± SE	826 ± 5.83	688 ± 8.81	533 ± 5.75	463 ± 2.53		54.6 ± 0.49	48.8 ± 0.49	44.5 ± 0.45	39.2 ± 0.60

ADDENDUM

In 1967 an experiment was conducted on California Gulls on an island in Joseph Lake (6 miles NW from Miquelon Lake) to test the relationship of growth and survival to the time of hatching of the chicks. Two plots A and B, in which California Gulls were nesting were selected approximately 50 feet by 30 feet each and were fenced with a wire mesh 2 1/2 feet high. Late clutches in plot A and early clutches in plot B were replaced by early and late clutches respectively from other locations of the island. The late clutches were obtained from a part of the island where all clutches had been removed on May 20 and new clutches started after that date were taken to replace early clutches in plot B. The fledging success and the body weights of the chicks in plots A and B, measured on July 16 and 31 respectively when the chicks were in their sixth week of life, are compared in Table 1.

Table 1 Comparative fledging success and body weights of early and late hatched chicks in 1967

Fledging success	Hatched June 7 - 10	Hatched June 23 - 27
No. nests	24	34
No. chicks hatched	72	60
No. chicks fledged	43	37
% chicks fledged	60	62
Weight in grams of chicks in their sixth week		
No. chicks weighed	41	36
Mean weight	601	633
Range in weight	270-820	450-890

It will be noted that chicks hatched late in the season survived as well and grew as rapidly as those hatched early in the season.

Whether the lower chick survival for late clutches in 1964 as compared with those in 1967 was caused by food shortage, predation or other factors can not be ascertained. Predation on the gull chicks in 1967 may have been curtailed by the wire mesh around the plots, which prevented chicks from

straying into the open where they are more subject to attack by adult gulls. Both plots were located in herbaceous cover which provided the gull chicks shelter against predation. Such predation was observed at Miquelon Lake in 1964 and 1965 on chicks, within their first two weeks of life, on the open beach and in the water. Paludan (1950) found the survival of Herring Gull chicks which hatched late in the season, was considerably lower than that of chicks hatched at the beginning. He stated that the demand for food generated by the rapid growth of the early chicks caused increased predation by their parents upon the small chicks which hatched later. Perhaps predation by the California Gulls, as observed by Paludan in the Herring Gulls, increased on small gull chicks with the progression of the 1964 breeding season.

Besides the wire mesh preventing predation, the chicks which hatched late in 1967 were raised by gulls which initiated laying at normal times compared to the naturally late nesters in 1964. In other gull populations (Coulson and White, 1958; Vermeer, 1963) it has been shown that late nesters are usually young and inexperienced birds or repeat layers whose initial clutches failed. Therefore, inexperience of the parents may also have contributed to lowering the survival of the late hatched chicks in 1964.

The results of the 1967 experiment do not provide evidence that a seasonally limited food supply governs the short breeding season of the inland nesting California and Ring-billed Gulls since both survival and growth of the late-hatched California Gull chicks was as good as that of those hatched earlier during the 1967 breeding season.

Coulson, J. C. and E. White, 1958.

The effect of age on the breeding biology of the Kittiwake *Rissa tridactyla* Ibis, 100: 40-51.

Paludan, K. 1951.

Contributions to the breeding biology of _Larus_ _argentatus_ and _Larus_ _fuscus_ Vidensk, Medd. Dansk. Naturh. Foren., 114: 1-128.

Vermeer, K. 1963

The breeding ecology of the Glaucous-winged gull (_Larus_ _glaucescens_) on Mandarte Island, B.C. Occ. Pap. B.C. Prov. Mus. 13. 104 pp.

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